LITTER PRODUCTION AND LITTER DECOMPOSITION IN A SCRUBLAND COMMUNITY

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by

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CONTENT

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ABSTRACT

1. Litter production and the process of decomposition were studied in a scrubland community using a single species of plant, Rhodomyrtus tomentosa, which is a very common shrub on hillsides in Hong Kong.
2. Litter collection was carried out at two sites. Litter was produced throughout the year with two peak falls, at the beginning and end of the dry season. The annual litter produced was 3640 kg $ha^{-1}yr^{-1}$.
3. During decomposition, the rate of loss of cations was faster than that of dry weight. The major loss occurred in the wet season. In one year, 38% of dry weight was lost. There was pronounced leaching of sodium and potassium: over 90% of each cation was lost in one wet season. A lesser amount of magnesium was lost. Calcium was relatively immobile, only 36% being lost in one year. Moreover, a considerable addition of calcium occurred during the wet season.
4. The mycoflora on the litter showed a successional change as it decayed. During early stages of decomposition, members of the phylloplane, such as Pestalotia sp. and Phialophora fastigiata, were most abundant. As decomposition progressed, they gave way to the soil species such as Trichoderma sp. and Mucor hiemalis. For the internal colonizers, the initial dominance of Colletotrichum sp. was taken over by Phomopsis sp.

5. The fauna showed an increase in abundance and species diversity as decomposition progressed. The most important groups of animals were the mites, collembolans, larval insects and adult flies from the family Chironomidae.
6. Chemical decomposition was brought about mainly by the mycoflora, while physical fragmentation was the major role of the fauna. However, the two aspects of the process could not be separated. The mycoflora and fauna interact in a number of ways to bring about decomposition, with environmental factors supplementing their action to a great extent.

INTRODUCTION

The importance of plant litter as a means of recycling nutrients within terrestial ecosystems has long been recognised. Studies on forest ecosystems began in the 1930s and included work on litter fall (Anon, 1932), nutrient content in litter (Alway and Zon, 1930) and litter decomposition (Melin, 1930). In subsequent years, especially in the 1950s and 1960s, there were intensive studies on litter decomposition and mineral recycling. These studies are carried on to-day and have resulted in numerous ecosystem models and quantitative nutrient budgets.

The role of the microflora and the fauna in litter decomposition has been elucidated. Of particular interest is the successive occurrence of the organisms concerned with decomposition. Through the studies on Pteridium petioles by Frankland (1966), on pine litter by Hayes (1965 b), on leaves of Fagus sylvatica by Hogg and Hudson (1966), and on Eucalyptus regnans leaves by Macauley and Thrower (1966), it has been established that there is a succession of the mycoflora on leaf litter. However, the trend is not so definite in the case of the fauna. Strenzke (1963) correlated the temporal change in the composition of the microarthropod population with the physical and chemical properties of the litter. Crossley and Hoglund (1962) and Crossley and Witkamp (1964) reported an initial invasion of tree litter confined in mesh bags by

a few species of invertebrate animals which became more diverse at later stages. However, Moeller (1965) suggested that the variation in abundance of animals may be associated with season rather than with succession per se. Anderson (1975) found no evidence for a pioneer fauna on leaves of Fagus or Castanea but he expected the faunal composition would change as decomposition progressed.

Most of the mineral recycling and successional studies have been concerned with forest ecosystems; some have been on grasslands (Curry, 1969) especially on pastures, while very few have been concerned with communities dominated by shrubs.

Scrubland is a very common type of vegetation in the Hong Kong countryside. Together with grassland, it dominates 59% of the total land surface (Hong Kong Government, 1968). Scrubland may represent a stage in succession to woodland but is usually found on soil of low fertility. It would be instructive to study how nutrients are released and recycled to maintain the community in its transition to the climax. The present project was designed as part of a larger project on overall nutrient cycling. It is an attempt to study the seasonal pattern of litter fall, the loss of dry weight and mineral ions, and the succession of the mycoflora and fauna during the process of litter decomposition. To facilitate manipulation, the leaves of a single species of plant, Rhodomyrtus tomentosa Hassk., were chosen for study.

Rhodomyrtus tomentosa Hassk. (Family Myrtaceae) is a common flowering shrub in Hong Kong, where it may be found from sea level to an altitude of more than 600 metres. It flowers in May and June and fruits in August and September. It may reach a height of 0.9 - 1.8 m. Its oblong leaves are opposite and shortly stalked, with a length of about 3.8 - 7.6 cm. Each leaf has three prominent main veins arising from near the base. The undersurface of leaf is densely covered with short and white woolly hairs. Rose-pink flowers are 2.5 - 5.1 cm in diameter. Each has five oval petals (about 1.3 cm long). The calyx-tube is hairy, having five lobes and two small bracts at the base. The stamens are numerous, and are pink with yellow anthers. Ripe fruits are dark purple in color, 1.3 cm across and are crowned with the persistent calyx. Many seeds are embedded inside the edible pulp and the fruit is eaten by birds and small mammals, and by man under the name of Shan Nim (山稔) (Figure 1).

Figure 1. Rhodomyrtus tomentosa Hassk.

CHAPTER 1

THE STUDY AREA

Location of the area

The study area is on the west-north-western slope of Tso Shan (Grassy Hill) (Figure 1.1), adjacent to the south-west edge of the Tai Po Kau Woodland. It has an altitude of 475 m. The location is shown in Figure 1.2 and the map reference is KV 079817 on sheet 2, series HM 50C, 1:50,000. The nearest urban area is Tai Po Market (population:29,400 in 1976) which is 3.6 Km away. The study area is 2.3 Km south-west of the Tai Po Kau Forestry Management Centre, from which the records of rainfall were derived. The Chinese University of Hong Kong campus is 4.4 Km to the east-north-east and other meteorological records were obtained from the station maintained by the Department of Geography there.

The area forms part of the catchment of a small river that flows approximately northward into Tai Po Hoi, near Tai Po Market (Figure 1.2). This area was chosen particularly for the study of nutrient input and output that was to have accompanied this work on litter decomposition. The working site was a series of slopes at an estimated angle of 26^{o}, separated by relatively flat ground having a slope of 8.5^{o}. The slopes may be vertical at places where there were out-crops of large boulders. The steepness of the slope was an impediment to some aspects of the present study.

Within this area a narrow Forestry Road, with restricted access, runs along the contour (about 460 m) from Tai Po Kau to Shing Mun Country Park. The work was carried out a few metres on the upper side of the road (Figure 1.3). Plant litter was collected at two sites and bags of litter for studying decomposition were set out nearby.

Weather

Mean monthly values of various meteorological elements for the 30 years 1947 - 1976 were obtained from the Hong Kong Royal Observatory and are given in Table 1.1, to show the weather conditions in Hong Kong. Hong Kong has broadly a dry season from October to March, and a wet season from April to September. The mean total rainfall for the year is approximately 2250 mm. The mean temperature is fairly high throughout the year, ranging from 15.6^{o}C to 28.5^{o}C. The colder period coincides with the dry season, while the hot period coincides with the wet season. Mean relative humidity was also fairly high (78%). The mean relative humidity of the driest month was only 14% lower than in the wettest month. The highest global radiation was recorded in the middle of the wet season. The greatest potential evapotranspiration was also recorded in the same month.

Monthly rainfall records at the Tai Po Kau Forestry Management Centre were also obtained from the Hong Kong Royal Observatory and are given in Table 1.2. The records show that the total rainfall at the Management Centre was slightly

higher than at the Royal Observatory; in general the distribution of rainfall throughout the year was similar to the Royal Observatory, except that May, June and October were much wetter, and July was much drier. The total rainfall for 1976 was about 14% above the mean for 16 years and, in general, the monthly distribution was more extreme with the drier months receiving much below the mean annual rainfall and the wetter months, receiving well above the mean. By contrast, the total rainfall for 1977 was about 10% below the mean over 16 years and all months, except July, September and October, were drier than normal. The rainfall in January and March of 1978 was higher than the mean for those months.

A maximum-minimum thermometer was placed 2.5 cm above ground level near the mesh bags used to study decomposition (Figure 1.4). Its readings for the maximum and minimum temperatures were recorded every four weeks. The maximum temperature in the dry season varied between 22°C and 24°C, while in the wet months it was 35°C to 37°C. The minimum temperature dropped to 1.5°C in January and February, but reached 22.5°C in July and September. The difference between the monthly maximum and minimum was greater in the dry season (22°C) than in the wet season (15°C) (Table 1.3).

Soil

The red-yellow podsolic soil at the site (Grant, 1960) has developed from coarse tuff of the Repulse Bay Formation (Allen and Stephens, 1971). The site is rocky, with frequent

outcrops of large boulders. The soil profile is simple, with three layers only; a brief description follows with the colors being given according to Munsell's system (1948):

0 - 7 cm: grey brown 2.5 Y 5/2 (moist: very dark grey brown 2.5 Y 3/2) which is penetrated by plant roots.

7 - 20 cm: light yellowish brown 10 YR 6/4 (moist: yellowish brown 10 YR 5/6). The boundary between this and the uppermost layer is indistinct. This layer has numerous inclusions of undecomposed parent materials.

20 - cm: yellow 10 YR 7/6 (moist: reddish yellow 7.5 YR 6/8) with some red nodular inclusions which is 10 R 6/6 (moist: red 10 R 4/6).

The parent material was more than 50 cm. below the surface.

During a preliminary study in August, 1976, the top 5 cm of soil had a pH of 4.5, the value for the 21 - 30 cm layer was 4.6 and the lowest layer had a higher pH of 4.7 - 4.8. Therefore, the top layers were slightly more acid than the bottom layers due to higher content of organic matter. The moisture content of the soil in the same month decreased down the profile, with 28.7% at the top 5 cm, 21.1% at the intermediate layer (21 - 30 cm), and 16.3% at the bottom layer (31 - 50 cm). The wetter condition and the lower pH were a result of plant growth.

Vegetation

The vegetation consists of a mixture of shrubs, herbs and grasses which make up three fairly distinct layers:

(i) The shrubs Rhodomyrtus tomentosa, Litsea rotundifolia, Raphiolepis indica and Daphniphyllum calycinum, together with the grass Miscanthus floridulus, which reach a mean height of 2.3 metres.

(ii) A mixture of fairly coarse plants such as Dicranopteris linearis, Blechnum orientale, Embelia laeta and smaller plants of Rhodomyrtus tomentosa. The mean height of this layer is 1.5 m.

(iii) A fairly dense ground layer, about 10 cm high, which is composed principally of Lindsaya ensifolia, Adiantum flabellulatum, Psychotria serpens, Utricularia sp. and Oplismenus sp.

The species present and the percentage cover were estimated by running a belt transect at a position between the sites of litter collection and litter decomposition. Thirty species were recorded (Table 1.4). The soil surface was almost completely covered with vegetation (total % cover = 145.7, bare ground = 3.6%), with the fern Dicranopteris linearis the most abundant species; its total % cover amounted to 43.6. In addition to living plants, dried up parts of Dicranopteris also amounted to 22.9%. Psychotria serpens too was of frequent occurrence, with a total % cover of 16.1. The third most abundant plants were the shrubs Rhodomyrtus tomentosa and Litsea rotundifolia,

having a total percentage cover of 12.7 and 14.3 respectively. Other common plants were the fern Blechnum orientale, Daphniphyllum calycinum, Embelia laeta, Raphiolepis indica, Rhus succedanea, Smilax china, and Zanthoxylum nitidum. Shrubs that were found outside the transect included Melastoma candidum and Phyllanthus emblica, and young specimens of the tree Liquidambar formosana. However, only very few species of grasses were found. The main species was Miscanthus floridulus which might reach the same height as the taller shrubs. It would seem, therefore, that the vegetation is a well-established scrubland which is showing little indication of change toward a woodland. In terms of structure and composition it resembles many other hillside scrublands in Hong Kong.

Study sites

The position of the sites was dictated by the availability of relatively flat ground within the sloping area. Three sites were selected, two for collection of litter, and one for setting out materials to study the process of decomposition (Figure 1.3).

At site 1 the quadrat for litter collection was placed under the canopy of the taller shrubs Litsea rotundifolia and the grass Miscanthus floridulus, and the smaller shrubs Viburnum sempervirens and Ardisia primulaefolia. Shorter plants included Adiantum flabellulatum and Psychotria serpens.

Site 2 for litter collection was about 4 - 5 m up the slope from site 1. The main plant above the quadrat was the

shrub Rhodomyrtus tomentosa. Others were Schefflera octophylla, Smilax china, Embelia laeta and Psychotria serpens.

The site for the decomposition study was the upper-most of the three. In a small clearing a reference metal stake (to which the mesh bags were tied) was placed (Figure 1.5). Thick scrub surrounded the clearing on all sides, and the vegetation was a mixture of Rhodomyrtus tomentosa, Melastoma sanguineum, Ilex asprella and Embelia laeta, together with some grasses. Of frequent occurrence was the fern Dicranopteris linearis. The mesh bags were placed under the thick vegetation 1 - 2 metres beyond the edge of the clearing (Figure 1.5).

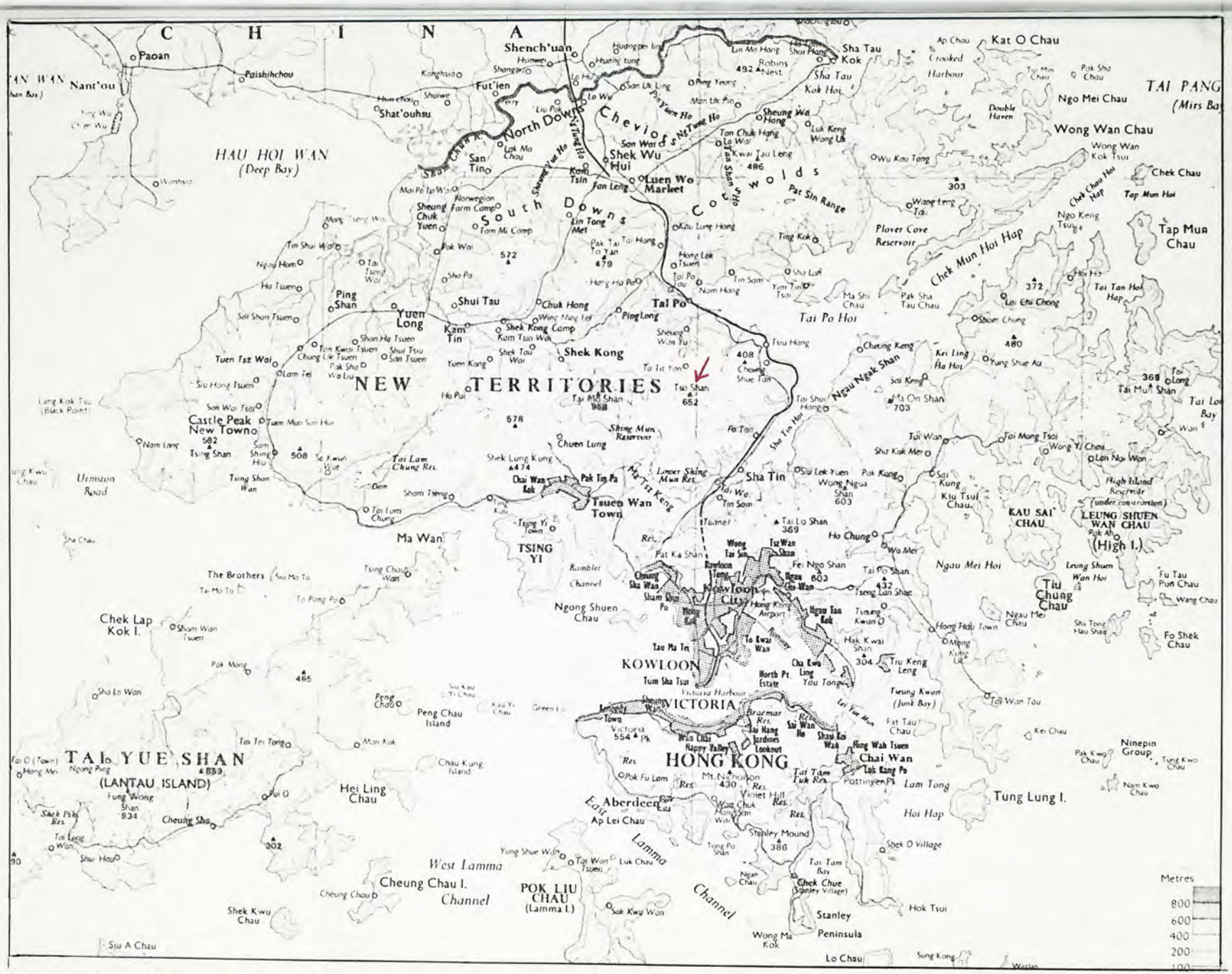

Figure 1.1 Map showing the location of the Study Area in relation to the rest of Hong Kong and the New Territories.
Scale : 1 : 250,000

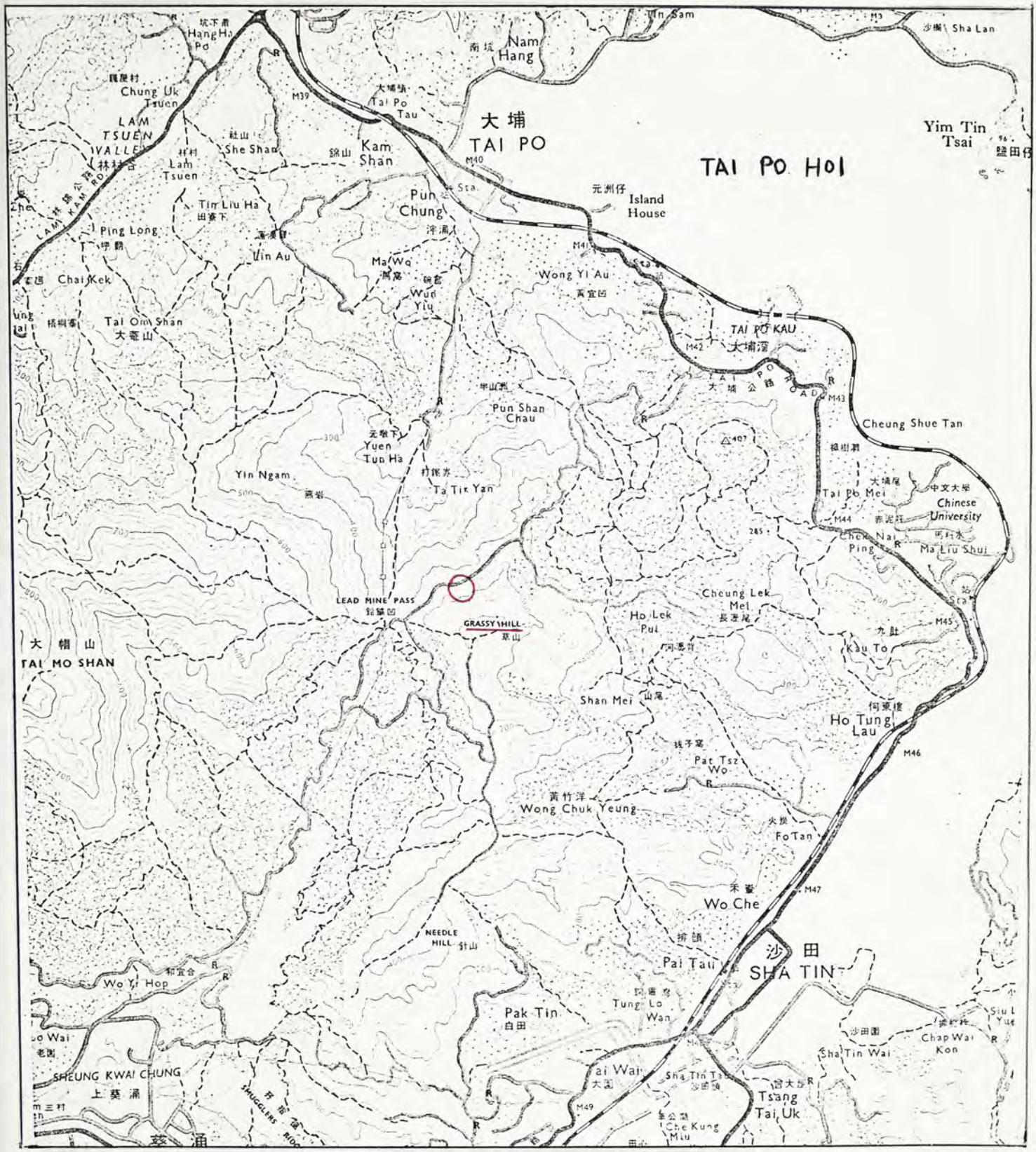

Figure 1.2 Map showing location of the Study Area.
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Scale : 1 : 50,000

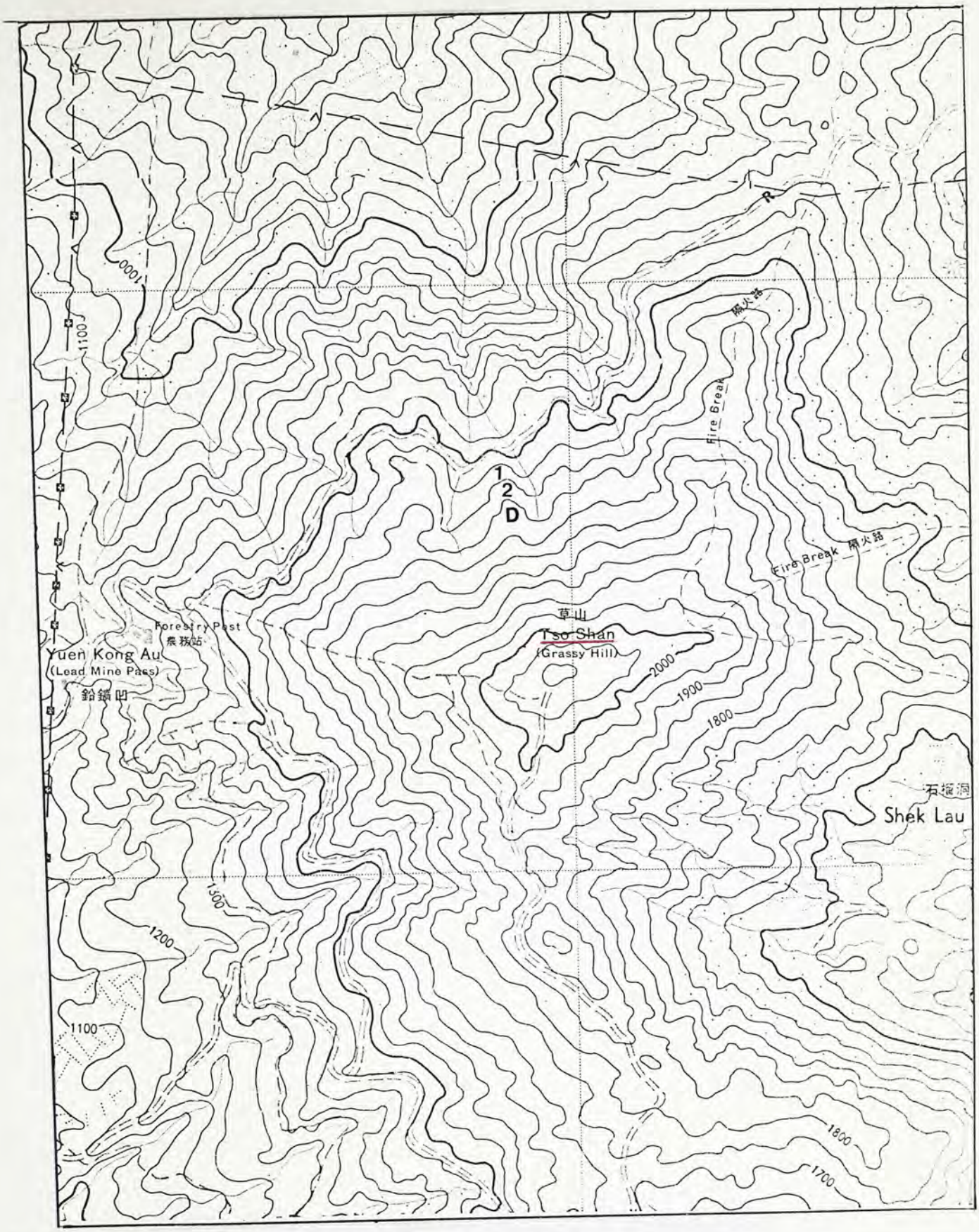


Figure 1.3 Map showing location of the Study Sites.
Sheet : 7B , Series : L884
Scale : 1 : 10,000
1, 2 : Litter Collection Sites 1 and 2
D : Site for studying decomposition.

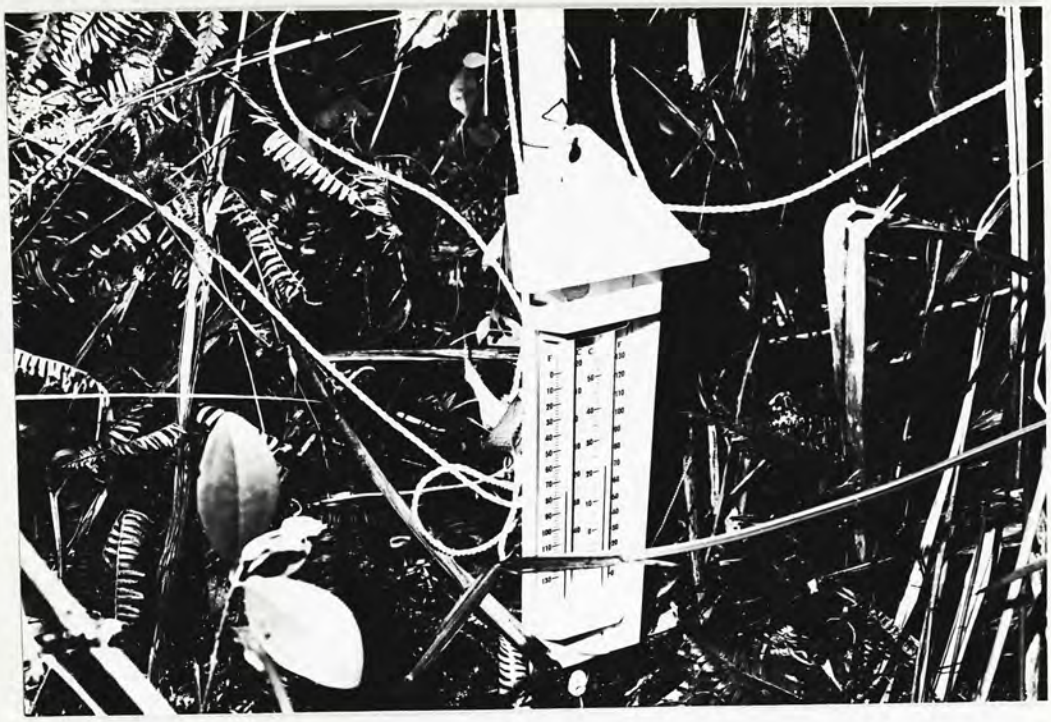


Figure 1.4 The maximum- minimum thermometer.

Figure 1.5 The reference metal stake and attached bags at litter decomposition site.

Table 1.1 Monthly normals of meteorological elements for the 30 years 1947 - 1976 at the Royal Observatory, Hong Kong.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total / Mean
Global radiation^{+} (MJm^{-2})	12.88	12.52	13.06	15.09	17.92	17.19	19.95	18.21	17.65	16.66	14.24	12.70	15.68
Mean temperature (°C)	15.6	15.9	18.4	21.9	25.9	27.6	28.5	28.1	27.5	24.9	21.3	17.5	22.8
Rainfall (mm)	28.5	44.9	49.3	135.3	289.3	457.5	319.3	420.2	330.8	107.2	38.2	25.9	2246.4
Mean relative humidity (%)	72	79	82	84	84	84	82	83	80	73	70	70	78
Potential evapo-transpiration*(mm)	81.6	74.2	87.3	100.1	130.0	131.6	152.2	145.9	134.3	128.6	104.0	86.3	1356.1

+ 1958 - 76 at King's Park , * 1952 - 76 at King's Park

Table 1.2 Monthly rainfall (mm) for 1976 - 78 at Tai Po Forestry Management Centre , compared with the mean for the same site.

Year / Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Mean (1960 - 75)	36.1	38.9	55.1	145.3	319.3*	523.4*	309.1	409.7*	231.3+	171.1	48.8	38.6	2327.1
1976	7.2	13.7	23.3	182.5	125.0	590.7	458.7	876.6	272.2	98.4	6.0	2.1	2656.4
1977	29.3	4.7	17.2	107.4	135.3	188.9	473.1	307.7	560.3	230.1	18.0	18.0	2090.0
1978	42.9	23.6**	94.9**	-	-	-	-	-	-	-	-	-	-

* Mean of 15 years , + Mean of 14 years.

** Data from the Chinese University of Hong Kong Campus.

Table 1.3 Maximum and minimum temperatures at the site (Figures refer to the previous period - usually 28 days duration).

Date of recording	Max.temp in°C	Min.temp in°C
1976. 26. Nov	31.0	7.0
23. Dec	23.0	5.0
1977. 20. Jan	23.5	1.5
15. Feb	22.0	1.5
17. Mar	29.0	5.5
14. Apr	32.0	8.0
12. May	36.5	15.0
9. Jun	36.0	20.5
19. Jul	37.5	22.5
10. Aug	36.5	21.5
1. Sep	37.0	22.5
30. Sep	35.0	18.0
3. Nov	-	-
28. Nov	-	-
28. Dec	24.0	7.0
1978. 26. Jan	23.0	2.5
23. Feb	25.0	7.5
23. Mar	26.5	9.0

Table 1.4 The vegetation and the total percentage cover (A belt transect, comprising 7 square metres, was run parallel to the road and adjacent to the litter collection site no. 2).

Species	Total % cover
1. Adiantum flabellulatum	0.7
2. Adina pilulifolia	2.9
3. Ardisia crispa	0.1
4. Ardisia primulaefolia	0.1
5. Blechnum orientale	5.4 (9.3 - dead)
6. Daphyniphyllum calycinum	5.6
7. Dendrotrophe sp.	1.0
8. Dicranopteris linearis	43.6 (22.9 - dead)
9. Dioscorea sp.	0.4
10. Embelia laeta	5.1
11. Ficus hirta	0.7
12. Hedyotis acutangula	0.1
13. Homalium sp. (?)	1.3
14. Lindsaya heterophylla	0.7
15. Lindsaya ensifolia	0.1
16. Litsea rotundifolia	14.3
17. Lonicera japonica	0.7
18. Loranthus macranthee	0.3
19. Miscanthus floridulus	9.3
20. Oplismenus compositus	1.1
21. Psychotria serpens	16.1
22. Raphiolepis indica	8.0
23. Rhodomrytus tomentosa	12.7
24. Rhus succedanea	5.0
25. Smilax china	4.3
26. Utricularia sp.	0.3
27. Viburnum sempervirens	1.0
28. Zanthoxylum nitidum	4.3
29. Unknown A (shrub)	0.3
30 Unknown B	0.1
Total	145.6
Bare ground	3.6
Mean max. height	2.3 m

CHAPTER 2

LITTER PRODUCTION

Litter production has been measured for a large number of study areas, particularly in forests. Bray and Gorham (1964) have compiled a comprehensive review of litter production in the forests of the world, and this has become a very useful reference on the subject. In general, there are two main approaches for the sampling of litter (Medwecka-Kornas, 1971). The first is the litter trap method: continuous trapping of the shed plant material and measuring the amount trapped over a fixed period of time. The second approach is the ground-litter sampling method: estimating the amount of litter in plots on the soil surface, so that the rate of turn-over can be determined. In the litter trap method, the traps may be randomly or systematically placed, and their number usually depends on the size of the area to be sampled.

Many different types of litter traps have been used (Newbould, 1967). They include nylon conical bags suspended from hoops raised above the soil surface, plastic buckets or dust bins with a terylene bag inside, square or rectangular trays with a wooden frame and nylon net at the bottom, and funnel-shaped traps above the soil surface with collecting chambers in the lower parts. The last type of trap is usually made of metal and is most useful for sampling seeds and fruits and for material from the ground flora. A survey of the

literature suggests that few studies have been made on production of litter in scrublands.

Materials and Methods

In this study, two 1.0 x 0.5 m (internal measurement) rectangular trays were used. The frame was made of wood 1.8 cm wide and 5.0 cm deep. One end of the frame was removable to enable the frame to be slipped through the vegetation to reach the soil surface, and the end-piece was then screwed into place. Three strips of 2.0 mm mesh nylon gauze were fastened beneath the frame (Figure 2.1).

Litter falling into the frame was collected at 4-weekly intervals for a period of 18 months. The strips of gauze were carefully detached from the frame, folded up and transferred to a large plastic bag for transport to the laboratory for dry weight determination. New strips of gauze were fastened to the wooden tray for the next month's collection.

Since the amount of litter was small and it was mostly made up of leaves, with only a few twigs, no attempt was made to separate it into components or different species of plants. In the laboratory, the litter was transferred to dried paper bags and put into the oven at a temperature of 85-90^{o}C. The process of dry weight determination took about six days (48 hour oven, 24 hour desiccator, weighing; 24 hour oven, 12 hour desiccator, weighing; and 24 hour oven, 12 hour desiccator, then weighing). The leaf materials had reached essentially

contant weight after this prolonged period of slow drying. Care was taken to standardize the period of drying and cooling because the paper bags absorbed moisture to a certain extent ($\pm$ 0.02 g).

In March 1978, after the last collection of litter, the plants above the quadrats were harvested. The area harvested was 1 m^2 and all of the leaves and other materials likely to contribute to the litter were taken. In the laboratory, the material was sorted into species, and the dry weight and moisture content were determined.

Results

The average dry weight, the percentage moisture in terms of field weight, and dry weight of litter at the two sites of collection are set out in Table 2.1. The moisture contents that exceed 100% on a dry-weight basis reflect heavy rain immediately preceding collection in the wet season. The biomass of the standing crops at the two sites at harvest is set out in Table 2.2.

a) Litter production at Site 1

The pattern of litter production throughout the period of collection is shown in Figure 2.2. The mean level of litter produced over 18 collections at Site 1 was 29.0 g m^{-2}. There were two pronounced peaks of production in the first year of collection. The first peak occurred in March and April, the end of the dry season; the second peak occurred in October,

the beginning of the dry season. The first peak in the second year of collection occurred in the same month as the previous year. (Collection was stopped after the first peak in the second year.) The peak production of litter was strikingly similar in both years, 47.3 g m^{-2} in the first year (recorded in the second peak) and 47.2 g m^{-2} in the second year (recorded in the first peak). However, the standard deviation for the mean litter production was large since low levels of production might be recorded in between the two peaks.

Leaves were the major component of litter. At Site 1 the litter was more heterogeneous than that of Site 2. Leaves of Litsea rotundifolia, Liquidambar formosana and Viburnum sempervirens were the major contributors. There was heavy fall of Litsea leaves in March and April contributing to the first peak fall in both years of collection. At the August collection of the first year, flowers from the grass Miscanthus floridulus became a component in addition to Litsea leaves and large amount of buds. The composition of litter at early November was similar to that in August, but with an additional component which came from insect attack on the stem of Litsea. The "dust" was fine enough for part of it to be lost through the 2 mm mesh of the nylon gauze.

b) Litter production at Site 2

The mean level of litter production for Site 2 was 25.2 g m^{-2} (Figure 2.3). There were also two peaks of production during the first year of collection. The first peak was recorded in

April and the second in October, at the same time as for Site 1. The first peak had not been reached during the second year of collection. A very low level of production was recorded at the last collection in March. This might be the prelude for the first peak of production in April. The peak production of litter was 53.3 g m^{-2}, slightly higher than that of Site 1. The standard deviation for the mean is similar to that of Site 1.

As noted before the litter at Site 2 was much more homogeneous than at Site 1. The usual components of litter were leaves from Rhodomyrtus tomentosa and Smilax china. At the June collection of the first year, the litter was made up almost entirely of petals of Rhodomyrtus flower. This might be caused by heavy showers of rain just before the collection. In early September, many fallen fruits of Rhodomyrtus were collected. Nearly all Rhodomyrtus fruits had dried up by the end of September. At the January collection of the year after, some dried Miscanthus leaves were collected in addition to the Smilax component.

c) Standing crop at Site 1

The total standing crop of leaves etc. at Site 1 at harvest was 744.60 g m^{-2} (Table 2.2). Litsea rotundifolia contributed more than half of the total biomass. Dicranopteris linearis was second in importance, accounting for about 30% of the total biomass. The rest of the plants were Miscanthus floridulus and seven other shrubs as listed.

d) Standing crop at Site 2

The total standing crop at Site 2 at harvest was 940.38 g m^{-2}. Dicranopteris linearis was the most important, and contributed about 63% of the total biomass. The next in importance was Rhodomyrtus tomentosa, followed by Smilax china and eight other species which accounted for the remainder of the biomass.

Discussion

Hong Kong is situated in the seasonally humid tropics (Thrower, 1975) with broadly a dry and a wet season. In terms of temperature there are four more-or-less distinct seasons. The dry season coincides with the cold season. The two observed peaks of litter fall corresponded to the beginning and end of the dry season. The onset of leaf senescence and abscission when the dry season comes may be caused by the water stress imposed on the plant (John, 1973), the plant having to shed a portion of its leaves to reduce the loss of water. At the end of the cold and dry season, favorable conditions allow new growth, so that the plant sheds the rest of its senescent leaves and makes new growth.

The main results for standing crop of leaves, and for production of litter, may be summarized as follows:

Site	Standing crop ($g\ m^{-2}$)	Annual litter fall ($g\ m^{-2}\ yr^{-1}$)	$\frac{\text{Litter fall}}{\text{Standing crop}}$ %
1	744.6	375.8	50.5
2	940.4	351.7	37.4

Thus, at a point in time the standing crop of leaves and materials other than woody stems was 2 - 3 times the annual litter fall. Consequently, a deduction might be that the average life of the leaves on the plants was also 2 - 3 years. The difference in the rate of turn-over in the two sites was because the dominant species of shrubs were different: Litsea was dominant at Site 1, while Rhodomyrtus was the most abundant component of litter at Site 2. Dicranopteris linearis was seldom collected in the quadrats although its standing crop was so great, because the whole plant dried up and seldom fragmented.

Calculated litter production from results at Site 1 was 3760 kg $ha^{-1}yr^{-1}$, and 3520 kg $ha^{-1}yr^{-1}$ at Site 2. The mean annual litter production for the two sites of collection was 3640 kg $ha^{-1}yr^{-1}$; and the mean litter production per 4 weeks was 270 kg $ha^{-1}yr^{-1}$. The individual values of the annual and monthly production at the two sites deviated very little from the mean. These results, together with the observation that the amount and the time of peak production of litter at Site 1 were similar, indicated that the present community was a fairly stable one.

The annual litter production at the study sites (3640 kg $ha^{-1}yr^{-1}$) was comparable to that obtained for heathland dominated by Calluna vulgaris, for Chapman (1967) obtained a value of 3180 kg $ha^{-1}yr^{-1}$ for Calluna (in southern England) at the age of 33 years (mature stage). Calluna litter regularly had portions of woody stem, short and long shoots, flower and bud as its

components. Nevertheless, leaf was the major component of litter from the present study and woody parts were seldom found. This may be attributed to the fact that the study area was well protected from prevailing winds.

Lossaint (1973) reported a value of 2300 kg $ha^{-1}yr^{-1}$ for a 17 year old garrigue community in southern France. The community was dominated by the evergreen shrub Quercus coccifera with a mean height of 1 m. Kittredge in 1955 (vide Mooney and Parsons, 1973) measured annual litter fall in the chamise chapparal at San Dimas in southern California, which was dominated by Adenostoma sp. and Ceanothus sp., he reported a value of 2800 kg $ha^{-1}yr^{-1}$.

In a study at a site 21 Km north of Wellington in New Zealand, Egunjobi (1971) reported a mean annual litter fall of 8880 kg ha^{-1} by a stand dominated by the spiny shrub Ulex europaeus. The mean height of the shrubs was 2.0 m. This figure was higher than any other figure so far recorded for warm-temperate shrubs or trees.

Except in the case of Ulex just cited, it seemed that the litter fall recorded in the present study was slightly higher than that obtained for other scrubland communities. Owing to the scarcity of available literature on litter production in communities dominated by shrubs, the average range of litter production in scrubland cannot be satisfactorily calculated. However, values of 2500 to 3500 kg $ha^{-1}yr^{-1}$ may be a reasonable estimate. Hence, litter production in scrublands is of a similar

order to that of the Cool Temperate Forests (3500 kg $ha^{-1}yr^{-1}$) (Bray and Gorham, 1964). When compared with Warm Temperate Forests, litter production in scrubland is much lower than the production by the mature forest (5500 kg $ha^{-1}yr^{-1}$) (Bray and Gorham, 1964), but may be similar to that by the young forest (3600 kg $ha^{-1}yr^{-1}$ for Eucalyptus maculata, McColl, 1966).

Figure 2.1 The quadrat for litter collection with nylon gauze in place.

Figure 2.2 Litter production at Site 1.

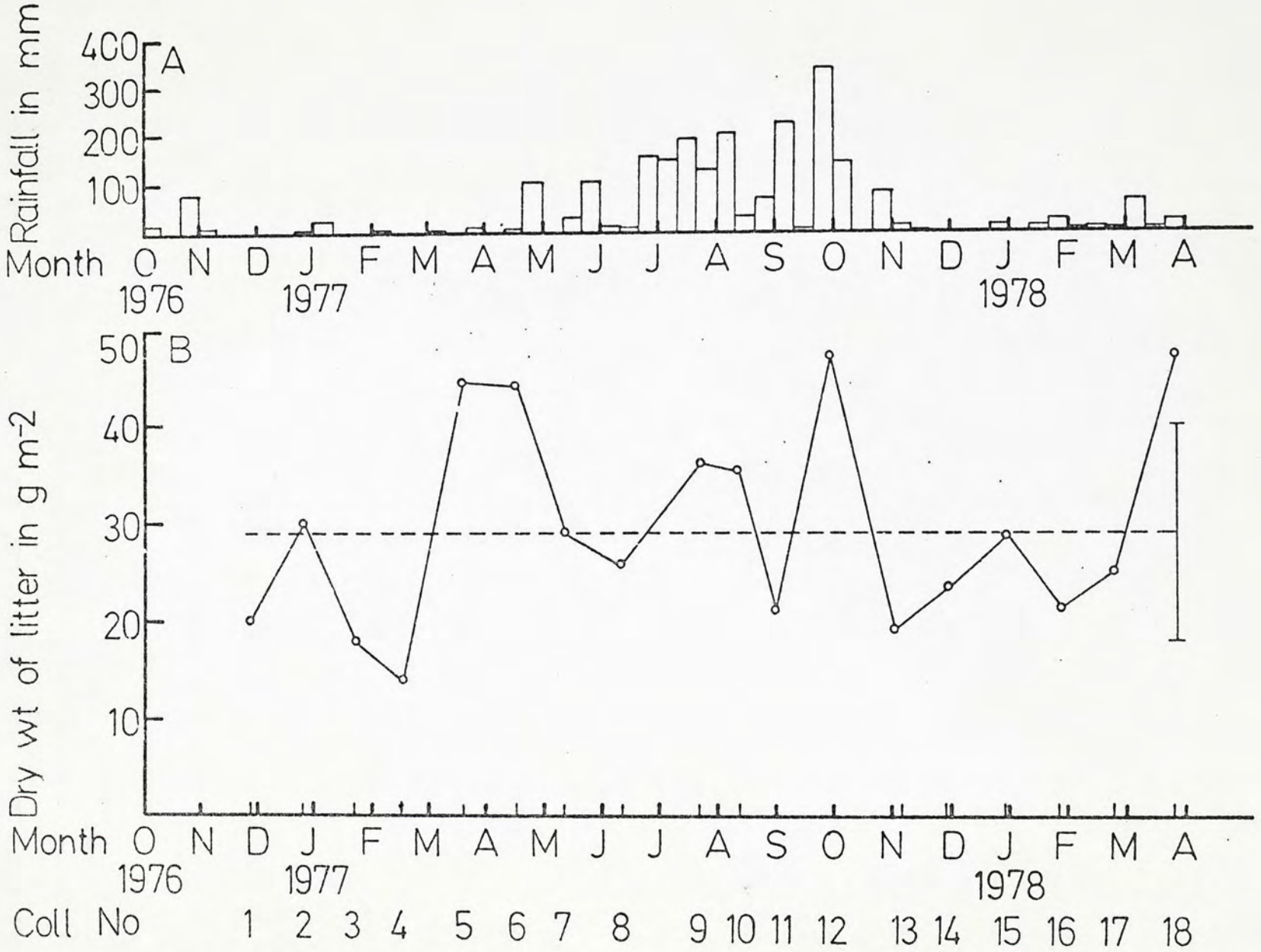

Rainfall in mm
400
300
200
100
A
Month O N D J F M A M J J A S O N D J F M A
1976
1977
1978
Dry wt of litter in g m-2
50
40
30
20
10
B
Month O N D J F M A M J J A S O N D J F M A
1976
1977
1978
Coll No 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18

Figure 2.3 Litter production at Site 2.

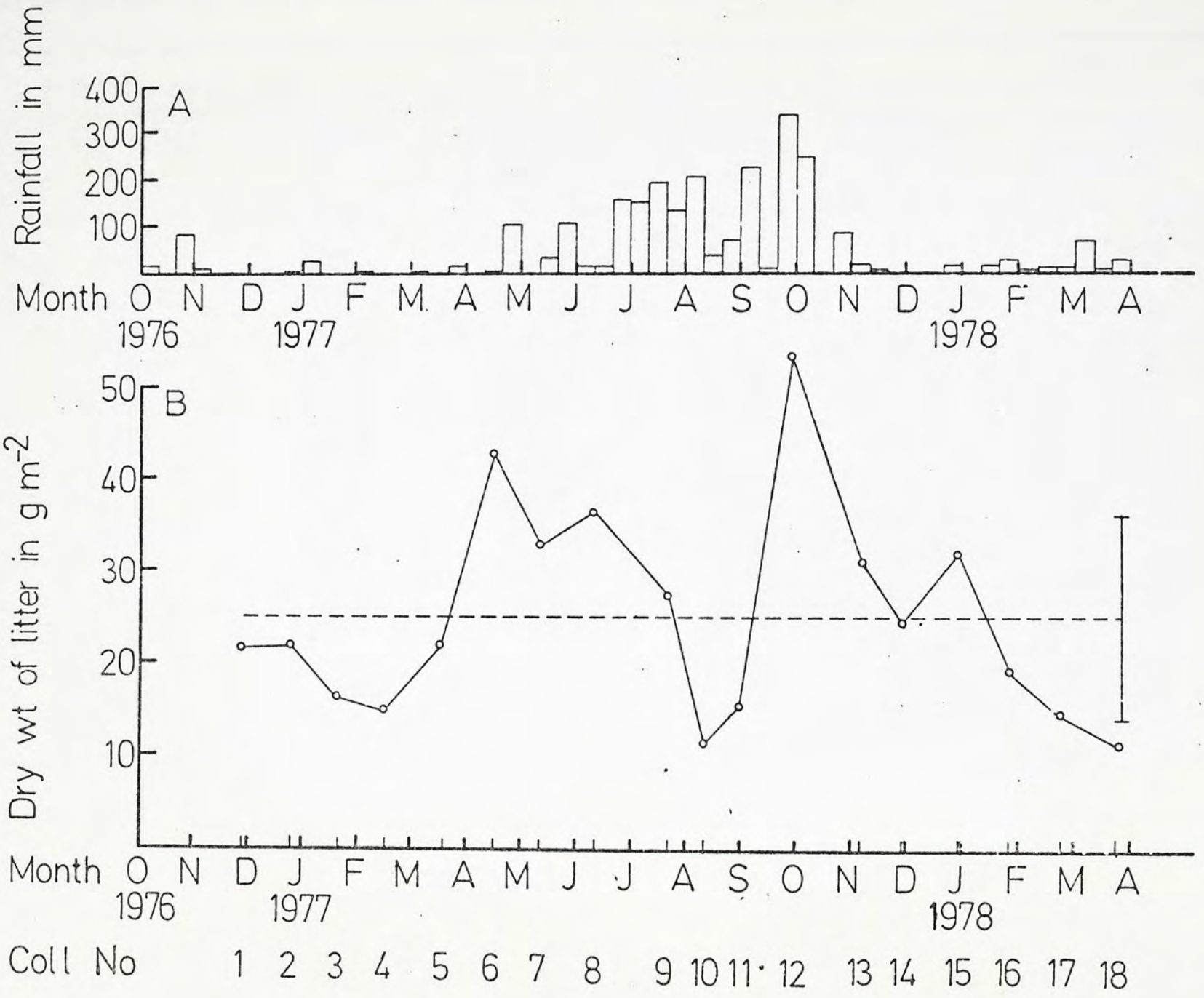

Rainfall in mm
400
300
200
100
A
Month O N D J F M A M J J A S O N D J F M A
1976
1977
1978
Dry wt of litter in g m-2
50
40
30
20
10
B
Month O N D J F M A M J J A S O N D J F M A
1976
1977
1978
Coll No 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18

Table 2.1 Litter production[@] and percentage moisture (on field and dry weight bases) at site 1 and site 2.

Date of Collection	Rainfall (mm) for previous 28 days	Site 1			Site 2		
		Average dry wt (gm^{-2})	% moisture on field wt basis	% moisture on dry wt basis	Average dry wt (gm^{-2})	% moisture on field wt basis	% moisture on dry wt basis
1976.26 Nov	30.7	20.6	14.33	16.73	21.43	12.85	14.75
23 Dec	0	30.19	28.40	39.66	21.96	28.44	39.75
1977.20 Jan	28.85	18.12	36.60	57.72	16.38	29.16	41.16
15 Feb	5.9	13.95	22.17	28.48	14.71	28.84	40.52
17 Mar	2.9	44.89	22.92	29.74	21.82	23.85	31.33
14 Apr	16.1	44.29	26.28	35.66	42.87	27.13	37.23
12 May	106.1	28.98	20.15	25.23	32.98	22.64	29.27
9 Jun	151.9	15.72	61.72	161.26	36.21	77.22	339.02
19 Jul	348.8	36.17	24.82	33.01	27.48	51.59	106.56
10 Aug	464.8	35.46	74.00	284.62	11.56	72.82	267.95
1 Sep	128.4	21.21	38.87	63.59	20.25	39.49	65.25
30 Sep	487.3	47.30	67.98	212.31	53.34	71.48	250.65
5 Nov	317.1	19.38	20.23	25.35	30.73	23.72	31.09
28 Nov	4.0	23.51	19.35	23.99	24.56	22.27	28.65
28 Dec	0	28.82	62.45	166.32	31.93	61.44	159.34
1978.26 Jan	36.9	21.31	24.46	32.38	19.24	25.96	35.06
23 Feb	43.1*	25.09	65.97	193.89	14.73	69.61	229.02
23 Mar	96.3*	47.23	73.56	278.15	11.40	76.66	328.37

Mean litter production for site 1 = 28.99 $\pm$ 11.13

Mean litter production for site 2 = 25.20 $\pm$ 11.21

@ Litter production is expressed in gm^{-2} on dry wt basis.

* Rainfall data from the Chinese University of Hong Kong Campus.

Table 2.2 Standing crop of leaves and other parts regularly added to litter on 23rd March, 1978.

Site 1	Biomass (in gm^{-2})
1. *Litsea rotundifolia*	397.67
2. *Dicranopteris linearis*	226.90
3. *Miscanthus floridulus*	27.36
4. Miscellaneous	92.67
(*Liquidambar formosana*	
Smilax china	
Psychotria serpens	
Viburnum sempervirens	
Lygodium japonica	
Chloranthus glaber	
Embelia laeta)	
5. Total	744.60
Site 2	
1. *Dicranopteris linearis*	588.79
2. *Rhodomyrtus tomentosa*	277.60
3. *Smilax china*	22.29
4. Miscellaneous	51.29
(*Psychotria serpens*	
Adiantum flabellulatum	
Smilax china	
Schefflera octophylla	
Chloranthus glaber	
Embelia laeta	
Melastoma candidum	
Pithecellobium sp.)	
5. Total	939.97

CHAPTER 3

LITTER DECOMPOSITION: LOSS OF DRY WEIGHT AND CATIONS

Studies of litter decomposition began with the observation of the Danish forester, P. E. Müller, on the soils of Fagus and Quercus woods and Calluna heaths of Denmark (vide Satchell, 1974). In his paper, published in 1879, Müller associated beech mull with thriving trees, and beech mor with unhealthy trees. Mull is granular forest humus that forms a layer of mixed organic matter and mineral soil and merges gradually into the mineral soil beneath; mor is forest humus that forms a layer of largely organic matter distinct from the mineral soil beneath (Woolf, 1977). Hesselman, in 1925, (vide Satchell, 1974) observed that mor could be formed by depressing the rate of litter decomposition and nitrogen mobilization. These and other early workers all recognized the importance of the plant cover in the formation of humus and the development of soil. We now know that the vegetation determines the properties of soil via litter fall and the rate of litter decomposition and mineralization, which in turn determines the magnitude of productivity.

The composition of litter, the loss of dry weight, the release of nutrient ions, the organisms involved, and the rate of the decomposition process and other related aspects have all been subjects for study. The production and composition of litter have been dealt with in Chapter 2, and the organisms involved will be the subjects of the next two chapters. This

chapter will be devoted to a consideration of the loss of dry weight and of cations, namely sodium, potassium, magnesium and calcium, by the litter during decomposition. An attempt will be made later to relate the rate and amount of loss to the activities of the mycoflora and the fauna.

A commonly-used method for the study of loss in dry weight and cations is to put weighed samples of litter into bags having mesh of specific sizes, and allowing the litter to decay on the forest floor. Samples are taken up for study at regular intervals. The mesh bags may be of nylon (Bocock and Gilbert, 1957; Bocock, 1964; Shanks and Olson, 1961; Witkamp and Crossley, 1966; and Maldague, 1967), of terylene (Madge, 1965) or of fibre-glass (Witkamp, 1966). Another method is to tether individual leaves by nylon threads and position them on the litter surface or deep within the litter layer (Witkamp and Olson, 1963; Woodwell and Marples, 1968).

Meshes of different sizes have been used. For example, Edwards and Heath (1963) used the following sizes:

7 mm: all micro-organisms and invertebrates could enter.

1 mm: earthworms excluded.

0.5 mm: only micro-organisms and small invertebrates (mites and springtails) could enter.

0.003 mm: all but micro-organisms excluded.

In the present study, 5 mm and 1 mm meshes were used. The former was used to study colonization by all soil animals, while the latter for study of colonization by micro-organisms

and small invertebrates.

Materials and Methods

The so-called litter-bag method was adopted, and the bags were made of nylon. Six mesh bags each measuring 14 x 14 cm were stitched with nylon thread onto a mesh tray (50 x 50 cm, supported on a steel frame). The bags were arranged in two rows (Figure 3.1). One row, and the mesh tray had a mesh size of 5 mm when stretched (coarse mesh) to allow entry of small and larger invertebrates. The second row had a mesh size of 1 mm (fine mesh) to study mainly the growth of micro-organisms and to restrict the entry to small invertebrates only. In each row, the first bag was used to measure the loss in dry weight, the second for loss in the cations sodium, potassium, magnesium and calcium, and the third for colonization studies.

a) Dry season samples

Preparation of samples

In October, 1976, fresh senescent leaves were picked from Rhodomyrtus plants growing in an almost pure stand about 200 m away from the site chosen for decomposition studies. Eleven grams (fresh weight) of leaves were put into the bags for dry weight and cation studies, while 22 grams were put into the bags for colonization studies. The mean moisture content of the leaves was determined from six replicate samples. The dry weight of the leaf samples in the bags was calculated from this.

Samples of leaves were also taken to determine their cation content.

Twelve trays of leaf samples were prepared; each was marked with an external indicator tied to one corner of the tray and an internal indicator put into one of the bags. These were the samples set out at the beginning of the dry season. They were taken to the site for decomposition studies on the day that the leaves were harvested, and were placed at random on the litter surface. Care was taken to press them downward to make good contact with the underlying litter. To facilitate locating the trays, they were tied to a reference metal stake in a clearing among the scrub (Figure 1.5).

Regular collections

Collections (or the taking up of the litter bags) were made at 4-weekly intervals except Collections Nos. 9, 10 and 11 (the interval between Nos. 8 and 9 was six weeks, while that between Nos. 9 and 10, 10 and 11 was three weeks). One tray was taken up at each collection. The two bags for colonization studies were immediately unfastened from the tray and transferred into separate plastic bags. The tray with the rest of the bags was transferred into another plastic bag. A sample of soil from beneath the tray being taken up was collected for extraction of invertebrates and the study of the soil mycoflora. Thus, a correlation could be made between

the organisms in soil and those colonizing the litter. The maximum and minimum temperatures during the period since the previous collection were read from the maximum - minimum thermometer tied to the reference stake (Figure 1.4).

At the stand where Rhodomyrtus leaves were harvested initially, fresh senescent leaves were again picked for studying the change of cation and mycoflora with season.

Processing in the laboratory

In the laboratory, the individual bags of leaves were processed as follows:

(i) Bag for studying colonization by small and larger invertebrates; transferred to Tullgren funnel for extraction (coarse mesh).

(ii) Bag for studying micro-organism colonization: plated out (fine mesh).

The detailed method of processing of (i) and (ii) will be described in Chapters 4 and 5.

(iii) Two bags for the study of loss in dry weight (coarse mesh and fine mesh): leaves were shaken free of soil particles and put into separate weighed paper bags which had been dried. These were dried in an oven at a temperature of 85-90^{o}C.

(iv) Two bags for nutrient studies (coarse and fine mesh): set out to air dry. When the leaves were sufficiently dry, they were shaken free of adhering soil particles

and ground in a Wiley mill with a No. 20 mesh screen. The ground material was further dried at a temperature of 50°C for 48 hours. The samples were then stored until analysis of cations could be done.

The soil sample was processed as follows:

(i) A portion was emptied into Tullgren funnel for extraction of animals alongside the litter sample (Chapter 5).

(ii) The rest of soil sample was plated on to agar media (Chapter 4).

Analysis for cations

When analysing for cations, the ground material was digested with a mixture of acids (Allen et al, 1972). About 0.25 g of material was weighed into a 100 ml Kjeldahl flask, 1 ml 60% perchloric acid ($HClO_4$), 4 ml conc. nitric acid (HNO_3) and 0.5 ml conc. sulphuric acid (H_2SO_4) were added. The mixture was swirled and digested slowly at moderate heat using a 4-position electric digestion rack. The heat was increased gradually. Digestion was continued for 15 minutes after the appearance of white fumes. When cool, the digest was diluted and filtered into a 50 ml volumetric flask and made up to volume. Blank digestions were carried out. The solutions were measured for sodium, potassium, magnesium and calcium contents by the A3600 Atomic Absorption, Emission or Fluorescence,

Spectrophotometer (Shandon Southern Instruments Limited). Sodium and potassium were measured with the Emission Mode, while magnesium and calcium were measured with the Absorption Mode.

b) Wet season samples

Fresh senescent leaves were collected at the end of March, 1977, at the same stand of Rhodomyrtus. They were allowed to air-dry in the laboratory and then put into bags as before. Five trays were put in the field in April. These constituted samples set out at the beginning of the wet season. The processing of these samples were exactly the same as the previous set. So that a comparison of loss in dry weight and cations can be made between samples set out in the dry and the wet seasons.

Results

a) Appearance of leaves

(i) In coarse-mesh bags in dry season

The leaves that were to be set out at the beginning of the dry season were picked in October, 1976. They were still quite green and healthy (Figure 3.2). After placing on the soil surface for 4 weeks, the leaves had become light to dark brown (Figure 3.3). At the third collection a number of dark leaf spots was observed, which might be the acervuli or pycnidia of colonizing fungi (Figure 3.4). At the fifth

collection, the dark color of the leaf began to fade and destruction of leaf skeleton occurred (Figure 3.5). The seventh collection coincided with the beginning of the wet season and, at this stage, the leaves had deteriorated markedly. Fragmentation occurred at the margins, and numerous faecal pellets were present on the leaves (Figure 3.6). At the ninth collection, most of the leaves had fragmented into pieces (Figure 3.7). At the eleventh collection (second last) virtually all leaves had become fragmented. The fragmented pieces were heavily contaminated with faecal pellets and soil particles (Figure 3.8).

(ii) In fine-mesh bags in dry season

For leaves from the fine-mesh bags, the process of decay was slower. At the tenth collection many of the leaves still retained their complete skeletal structure though they had become very brittle. The leaves began to fragment only at the eleventh collection. Furthermore, they were less contaminated with soil particles or faecal pellets.

(iii) In coarse-mesh bags in wet season

Leaves that were set out at the beginning of the wet season were picked in March 1977, when old leaves still persisted. Therefore there were reddish-brown patches among the green color of the leaves. Some leaf spots were observed. After being on the soil

surface for 4 weeks, the color of the leaves darkened (Figure 3.9). Destruction of leaf structure occurred and the leaves were heavily contaminated with soil particles which may be the result of deposition from heavy runoffs. Similar conditions persisted at the second collection (Figure 3.10). At the third collection, the leaves were already fragmented to a great extent. Mycelial growth was visible to the naked eye in addition to the heavy contamination with soil particles and faecal pellets (Figure 3.11). At the fourth collection, the leaves were so extensively fragmented that they appeared similar to those which had been placed on the soil surface for eleven months (Figure 3.12). The process of fragmentation and decay was markedly accelerated in the wet season.

(iv) In fine-mesh bags in wet season

As for leaves in fine-mesh bags set out in the dry season, these leaves were much less fragmented than those in the corresponding coarse-mesh bags.

b) Loss of dry weight

The moisture content of leaf samples at collection varied with the atmosphere and relative humidity, and moisture content of the overlying litter, though slightly wetter conditions existed inside the mesh bags. In general, wetter conditions were recorded inside fine-mesh than coarse-mesh bags.

(i) Samples in the dry season

The pattern of loss in dry weight in both coarse and fine-mesh bags was strikingly similar. During the first six months, which coincided with the dry and cold season, there was gradual but slight weight loss. The maximum loss during this period was only about 10% of the initial weight. However, the weight loss was rapid when the wet season came (Figure 3.13). Between the sixth and tenth collections, the net loss amounted to 33% (Table 3.1). From then on, the loss was more gradual. The loss from the coarse-mesh bag in the eleventh collection reached 49.35%, and this was due to the loss of fragmented material through the mesh.

(ii) Samples in the wet season

The pattern of loss both from the coarse and fine-mesh bags followed closely the set in the dry season, except that the initial loss in dry weight was very great (Figure 3.13). The loss in weight in five months of the wet season was the same as in twelve months of the dry season. Therefore, it was tempting to infer that moisture was the effective agent causing the loss in dry weight.

c) Seasonal variation in cation content

Fresh senescent leaves were harvested from the same pure stand of Rhodomyrtus every month on the day when the regular

collections were made. They were analysed for cation content in order to investigate the seasonal variation. The results are given in Table 3.2 and Figure 3.14. The levels of sodium and magnesium remained at a steady value throughout the year (Figure 3.14), and the value varied from 0.45 mg/g leaf tissue to 0.62 mg/g for sodium, and 0.93 mg/g to 1.08 mg/g for magnesium. However, there was a very small depression at the end of the dry season in March (for sodium) and April (for magnesium).

The content of potassium and calcium fluctuated somewhat. Potassium varied from 5.12 mg/g to 8.42 mg/g and the higher content was observed during the dry season. There was a pronounced depression at the end of the dry period in April and May (Figure 3.14). Thereafter the level of potassium rose in the wet season but was still lower than in the dry season. The lower level of potassium may be due to leaching from the leaf surface.

Calcium content varied from 3.11 mg/g to 4.68 mg/g. There was a similar depression to potassium at the end of the dry season in April. However, the levels of calcium was just opposite to that of potassium. There was lower level in the dry season but slightly higher levels in the wet season (Figure 3.14).

d) Change in cation content during decomposition

(i) Change in the dry season

The variation of the four cations throughout the process of decomposition showed a more or less similar pattern (Figures 3.15, 3.16, 3.17 and 3.18). The cation content fluctuated, and there were increases in the first few collections followed by a gradual loss until, at the beginning of the wet season, there was a marked loss. The loss may reach 90% or more. It was then followed by a steady loss or a slight increase (relative to the lowest percentage loss) in the last few collections.

Sodium. A marked loss of sodium from samples in coarse-mesh bags occurred in April. The percentage loss reached its highest levels of 87% and 89% relative to the sodium content of the initial sample in June and July. From then on there was a little relative increase.

The change in fine-mesh bags was similar except that the highest percentage loss was slightly higher. The value reached in the last collection was similar in the two different mesh-sizes.

Potassium. The time of marked loss in potassium in coarse-mesh bags occurred at about the same time as sodium. By the ninth collection (July), more than 90% of the initial potassium had been lost. In

general, the loss in potassium was greater than the loss in sodium.

The level of loss in fine-mesh bags reached the same value as in the coarse-mesh bags.

Magnesium. The initial addition of magnesium in coarse-mesh bags was fairly great (29%). Then there were gradual losses until in June when the loss was fairly rapid. The greatest percentage loss was about 88%, slightly lower than the corresponding values for sodium and potassium.

However, the loss was not so rapid in fine-mesh bags. The highest percentage loss was about 10% lower than in coarse-mesh bags.

Calcium. Calcium behaved differently from the other three cations. There was addition in coarse-mesh bags throughout until at the tenth collection. The highest percentage loss was only 45% in the second last collection.

In the fine-mesh bags, there was addition until the eleventh collection. The highest percentage loss was about 10% lower than in the coarse-mesh bags.

(ii) Change in the wet season

The variation of the four cations resembled closely the latter part of the pattern for samples set out in the dry season (Figures 3.15, 3.16, 3.17 and 3.18). However, there was no initial addition except for

calcium. Rather there was rapid loss at the very beginning, which was followed by a more gradual decline.

Sodium. There was great initial loss in the coarse-mesh bags. The percentage loss reached 90% at the third collection. The greatest percentage loss was 98%. The litter sample had only a very small amount of sodium left at the last collection.

The magnitude of loss in the fine-mesh bags was similar to the coarse-mesh bags.

Potassium. The loss in coarse-mesh bags was also very rapid, although it was lower than the loss in sodium. The greatest percentage loss was only slightly lower than sodium.

The magnitude of loss in fine-mesh bags was similar to that in the coarse-mesh bags.

Magnesium. Loss in coarse-mesh bags was gradual and less rapid than in the case of sodium and potassium. The greatest percentage loss was only 55%, much lower than in the dry season.

Loss from samples in the fine-mesh bags was slightly lower than from the coarse-mesh bags.

Calcium. As the change in the dry season, there was gain or addition in calcium in samples inside coarse-mesh bags throughout the collections with peak percentage gain at the second collection. The

percentage gain was higher than in the dry season.

The pattern of change in the fine-mesh bags was similar to that in coarse-mesh bags. The peak percentage gain occurred at the third collection. The percentage gain was slightly higher than in the coarse-mesh bags.

Discussion

Fresh senescent leaves were used as the starting material for the first set of experiments. The dry weight of leaves being used was calculated by extrapolation. However, the moisture content of individual samples may deviate slightly from the mean dry weight obtained. This explains why, during the first few samples, the dry weight at collection may be greater than the initial weight. Therefore, for the second set of experiments the starting leaf material was air-dried. However, air-dried leaves suffered from the disadvantage that they deviated more from natural conditions.

Other reasons for increases in the dry weight of the contents of litter bags have been suggested. For example, Gosz et al (1973) studied the nutrient release during decomposition in the Hubbard Brook Forest and reported an absolute increase in the weight of leaves at the beginning of the warm season (June). The main species of trees studied were Acer saccharum, Fagus grandiofolia and Betula allegheniensis. They suggested a possible reason for the increase may be contam-

ination by current litter fall and increase in the population of decomposing heterotrophs. The fall of bud scales, flowers and pollens was great at that time (Gosz et al, 1972) and these materials were small enough to enter the 3 mm holes of the mesh bags and mix with the leaf samples. In the present study, a large portion of the litter found above the mesh tray was dried Dicranopteris linearis. Contamination by this material was unlikely because it did not fragment easily. However, many light brown seeds were observed mixed with the leaf samples in the coarse-mesh bags. Furthermore, during the later stages of decomposition, contamination by lumps of soil and adhesion of faecal pellets became important in contributing to the dry weight. The extent of increase due to the decomposing heterotrophs was more difficult to estimate. Consequently, the absolute loss of dry weight may be greater than observed.

It was observed that the cation content of leaves harvested freshly each month showed a depression at the end of the dry season. The depression in cation content was more pronounced for potassium and calcium but less so for sodium and magnesium. This pattern of change of cations may be correlated with the pattern of growth of the Rhodomyrtus plant. Senescence and fall of leaves extended over the entire dry period and the leaves became reddish brown in late November. The browning persisted until May of the following year, when new green leaves appeared and the plant began to flower. Fruit was set in late June and July, and became fully ripe in August.

Fruits started to dry up in September completing a year's growth (observation from the present study). The depression of cation content coincided with the end of senescence. Cation content began to rise as new growth was started and then remained at a steady level thereafter. This sequence suggests that, as the new leaves are forming, the cations are either taken up directly from the soil solution or mobilized within the plant, and moved to the expanding leaves.

For sodium and potassium the magnitude of loss in the coarse and fine-mesh bags was similar. However, in the case of magnesium and calcium the loss was less in fine-mesh bags than in coarse-mesh bags. When there was gain in calcium, the percentage gain was greater in the fine-mesh bags than in coarse-mesh bags.

The rate of loss and the percentage loss of sodium were closely similar to that of potassium. The percentage loss of magnesium was comparable to sodium and potassium, but the rate of loss was much lower. For calcium, both the rate of loss and the percentage loss were lower than for other cations. Appreciable loss of calcium occurred only during the last three collections and the highest percentage loss was only half of that of the other three cations. The less rapid loss of calcium can be explained by the observation that it was one of the structural elements (found in the middle lamellae of plant cells as calcium pectate), as suggested by Gosz et al in 1973, and therefore it was not leached. An appreciable amount was

lost only when the structure of the leaf disintegrated. However, both sodium and potassium showed rapid initial leaching when samples were set out in the wet season. These results agreed well with studies on the loss of nutrient elements on decomposition by Attiwill (1967) and Ewel (1976), except that the rate of loss of calcium was greater than that of magnesium. The mobility of ions in decomposing litter calculated by Attiwill was in the order Na>K>Ca>Mg. The higher the mobility, the quicker were the ions lost.

In the present study, there was addition of calcium until the ninth or tenth collection . It was possible that addition came with the rain because there was a slight increase in the calcium content of green leaves in the wet season. Surface runoff may also add to the mesh bags since they were placed in contact with the soil surface. Immobilization of nutrients by micro-organisms may also add to the concentration of ions in the litter (Ausmus, Edwards and Witkamp, 1976).

Climatic factors played an important role in determining the rate of decomposition (Wong, 1975). Samples set out at the beginning of the dry season lay more or less intact for the first six months, but began to lose more dry weight and cations at the beginning of the wet season. Samples set out at the beginning of the wet season started losing dry weight and cations almost immediately. Consequently, the amount of material lost relative to the initial amount by the wet-season set in five months' time was almost equal to the amount lost relative

to the initial amount by the dry-season set in twelve months. The rate of decomposition of the wet-season set was more than double that of the dry-season set.

Fresh senescent leaves were used as the starting material for litter samples set out in the dry season, while air-dried leaves were used for litter samples set out in the wet season. Strictly speaking, these two sets might not be comparable. However, we can examine leaves taken up at the seventh collection in the dry season and those taken up at the first collection of the wet season (the time of collection of these two coincided) (Figures 3.6 and 3.9), and start our comparison from this point. Leaves from the seventh collection of the dry-season set had already begun to fragment, while leaves from the first collection of the wet-season set were still intact, resembling leaves from the third collection of the dry season (Figure 3.4). At this stage, we can say that leaves from the seventh collection (dry season) were at a more advanced stage of decay than those from the first collection (wet season). However, when we compare leaves from the ninth collection of the dry season and from the third collection of the wet season, the degree of fragmentation of the two samples was closely similar. Leaves from the fourth collection in the wet season were so fragmented that they resembled leaves in the eleventh collection of the dry-season set. This brought out the importance of moisture in accelerating the decomposition rate. Unfortunately, the local dry season coincided with the period of low temperature, so that

the influence of these two parameters (moisture and temperature) could not be studied independently in the field.

Temperature in Hong Kong is fairly high throughout the year. The difference between the monthly mean maximum and minimum temperatures was about 5°C throughout the year. There was a 20°C difference between the yearly mean maximum and minimum (Figure 3.13). Therefore, the lowering of temperature in the dry season may not be a limiting factor inhibiting the decomposition of leaves because the minimum temperatures were not very low (in biological terms) and the duration for which they persisted was short. Nevertheless, the higher temperature in the wet season under local conditions may supplement the effect of high moisture to cause more rapid loss in both dry weight and ions.

In the seasonal tropics, rainfall and moisture content were more likely to be the limiting factor (Madge, 1965; Hopkins, 1966). However, in the temperate or cool-temperate regions, rainfall or temperature may be the limiting factor, depending on local conditions (Edwards and Heath, 1963; van der Drift, 1963). For example, Mikola (1960) studied the decomposition rate in southern and northern Finland and found that the loss of dry weight from litter samples in southern Finland was 40% more than that in northern Finland. Therefore he concluded that temperature was the limiting factor in the cool-temperate regions.

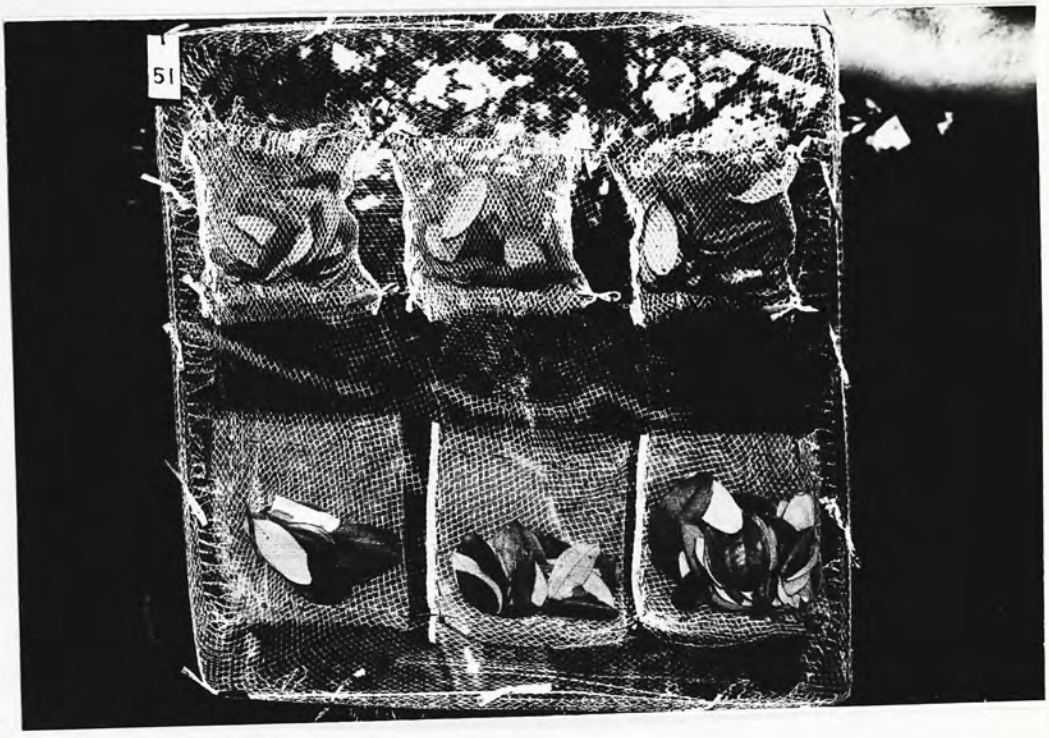


Figure 3.1 The coarse and fine mesh bags stitched to the mesh tray (actual size = 50 x 50 cm).

Figure 3.2 Fresh senescent leaves used as starting material to study decomposition in the dry season (approx. length of largest leaf = 7.3 cm).

Figure 3.3 Physical appearence of leaves from the coarse mesh at the first collection in the dry season.

Figure 3.4 Physical appearence of leaves from the coarse mesh at the third collection in the dry season.

Figure 3.5 Physical appearence of leaves from the coarse mesh at the fifth collection in the dry season.

Figure 3.6 Physical appearence of leaves from the coarse mesh at the seventh collection in the dry season.

Figure 3.7 Physical appearence of leaves from the coarse mesh at the ninth collection in the dry season.

Figure 3.8 Physical appearence of leaves from the coarse mesh at the eleventh (second last) collection in the dry season.

Figure 3.9 Physical appearence of leaves from the coarse mesh at the first collection in the wet season.

Figure 3.10 Physical appearence of leaves from the coarse mesh at the second collection in the wet season.

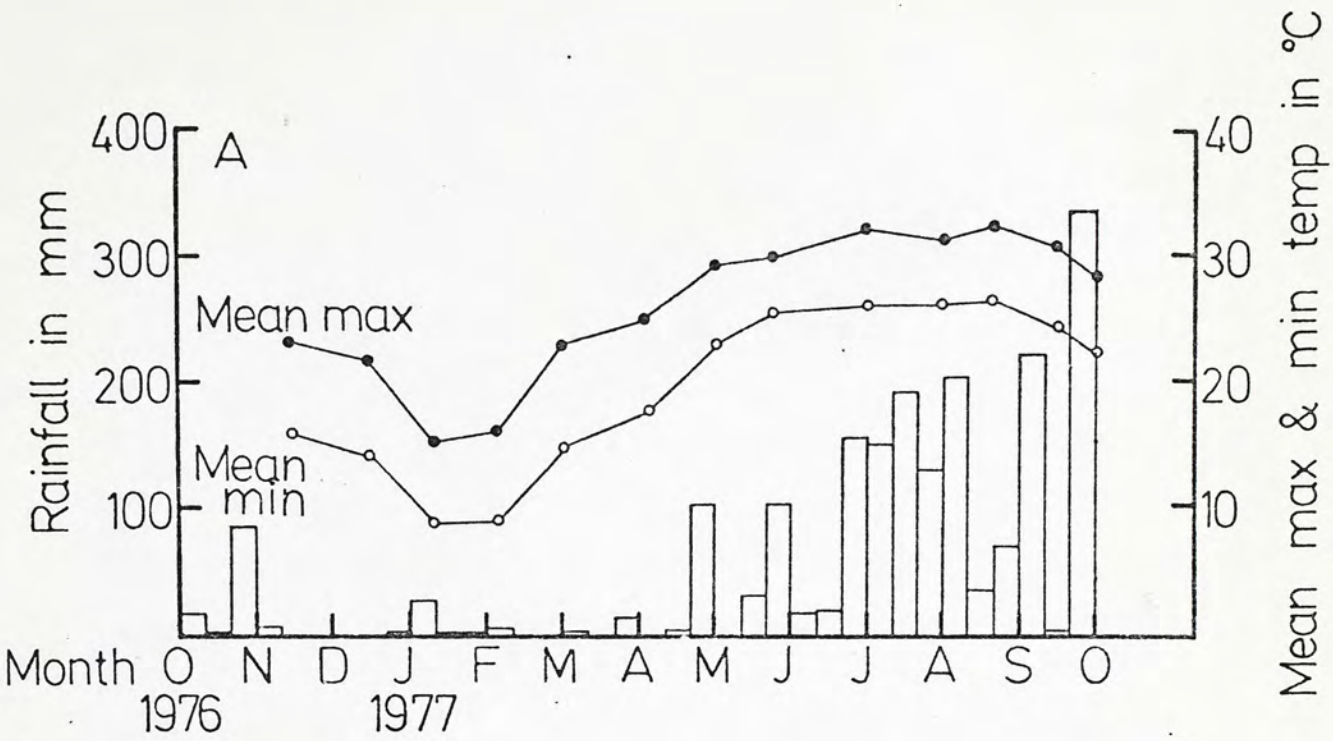
Figure 3.11 Physical appearence of leaves from the coarse mesh at the third collection in the wet season.

Figure 3.12 Physical appearence of leaves from the coarse mesh at the fourth collection in the wet season.

Figure 3.13 Percentage loss in dry weight of litter samples set out in the dry and wet seasons.

(Percentage loss is expressed with reference to the initial dry weight.)

∘——∘ dry season litter in coarse - mesh bags
▲——▲ dry season litter in fine - mesh bags
∘- - -∘ wet season litter in coarse - mesh bags
△- - -△ wet season litter in fine - mesh bags


A
Rainfall in mm
400
300
200
100
Mean max
Mean min
40
30
20
10
Mean max & min temp in °C
Month O N D J F M A M J J A S O
1976
1977

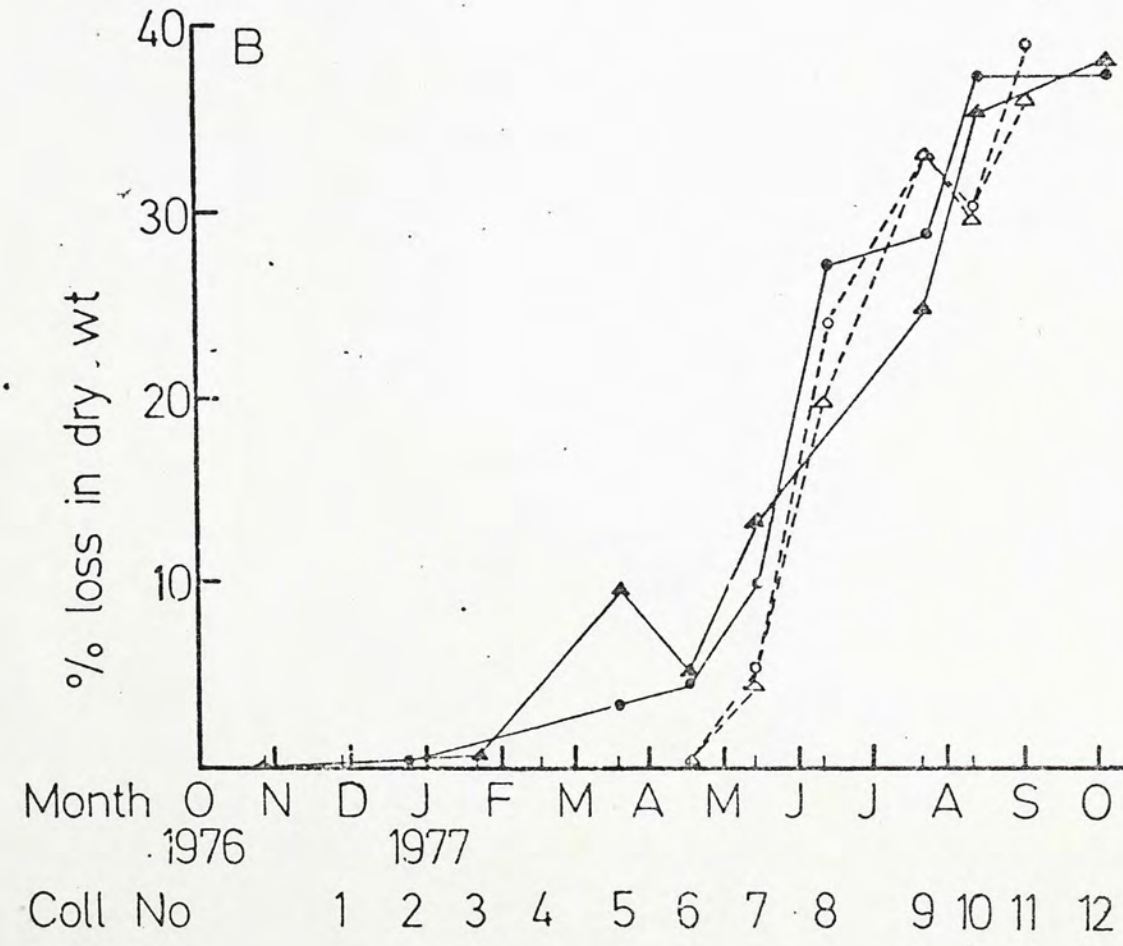
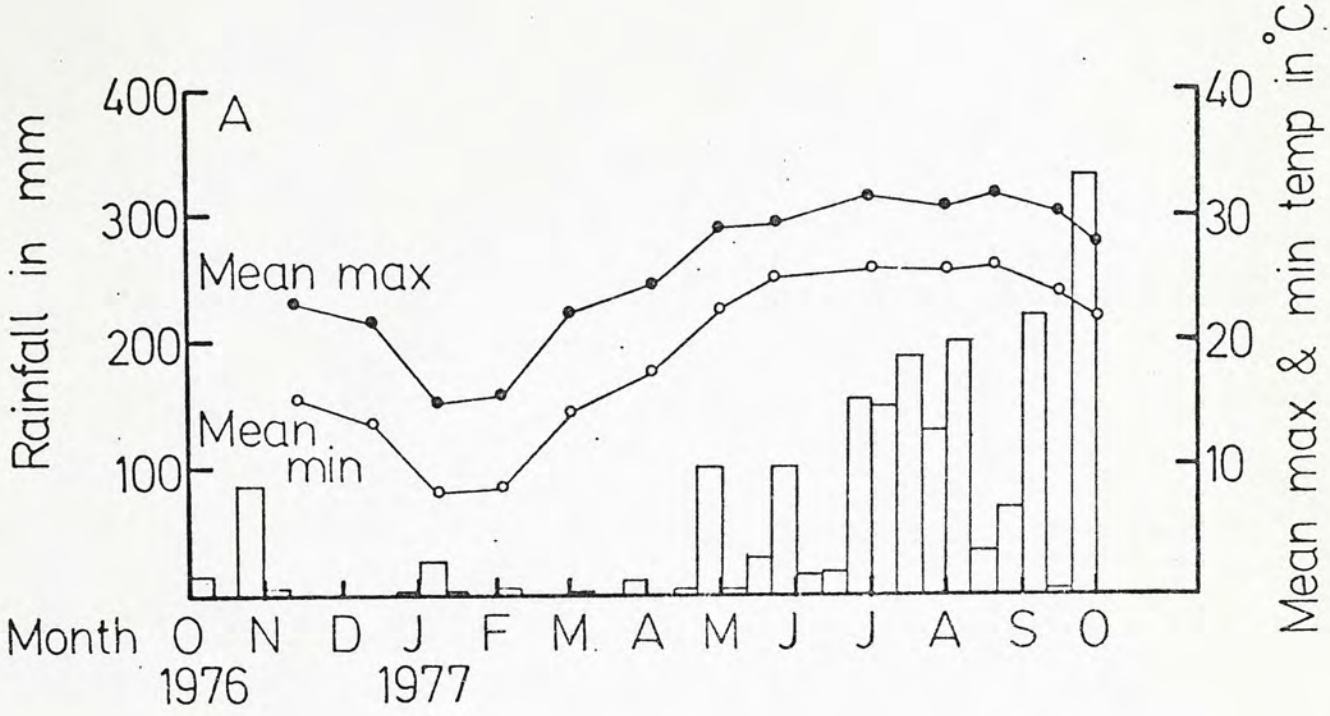

B
% loss in dry. wt
40
30
20
10
Month O N D J F M A M J J A S O
1976
1977
Coll No 1 2 3 4 5 6 7 8 9 10 11 12

Figure 3.14 Seasonal variation in cation content of fresh senescent leaves (control leaves).


A
Rainfall in mm
400
300
200
100
Mean max
Mean min
40
30
20
10
Mean max & min temp in °C
Month O N D J F M A M J J A S O
1976
1977

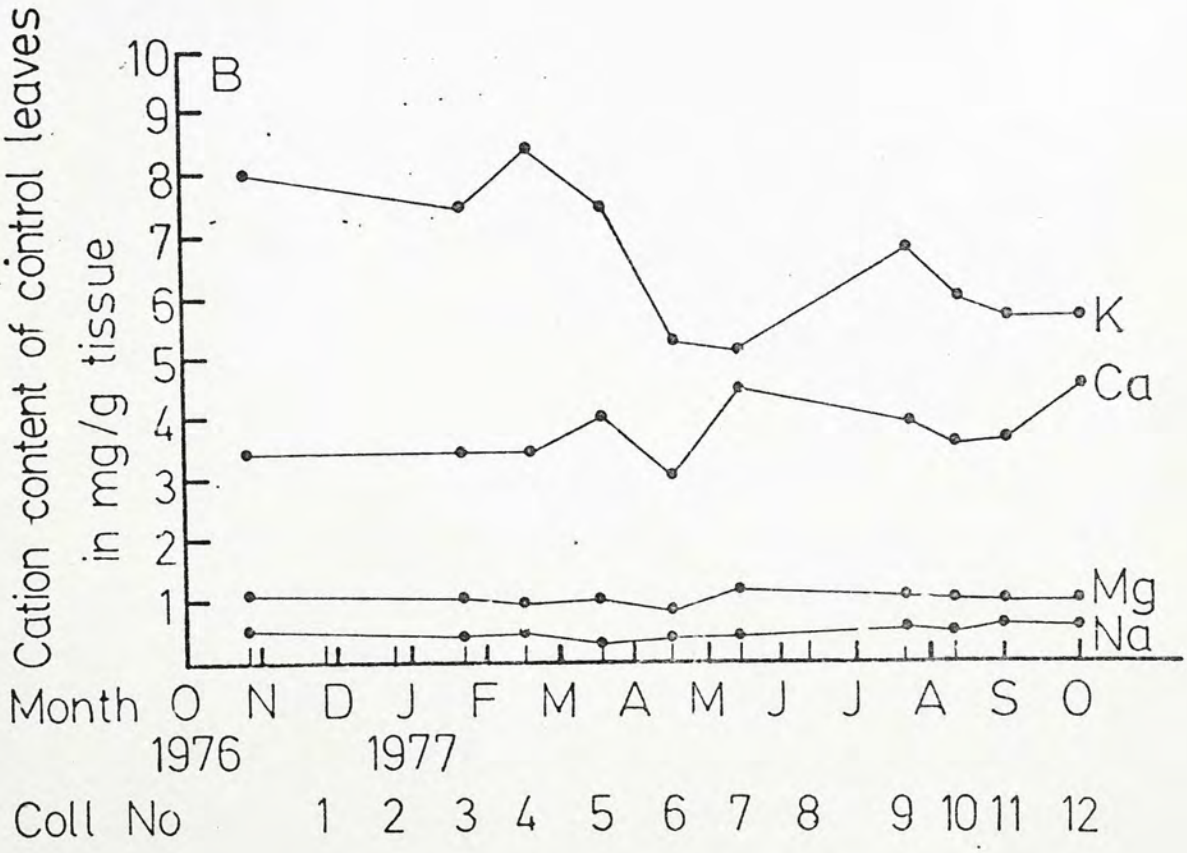

B
Cation content of control leaves
in mg/g tissue
10
9
8
7
6
5
4
3
2
1
K
Ca
Mg
Na
Month O N D J F M A M J J A S O
1976
1977
Coll No 1 2 3 4 5 6 7 8 9 10 11 12

Figure 3.15 Percentage change in sodium content of litter samples set out in the dry and wet seasons.

(Percentage change is expressed with reference to the initial sodium content.)

o——o dry season litter in coarse - mesh bags
Δ——Δ dry season litter in fine - mesh bags
o- - -o wet season litter in coarse - mesh bags
Δ- - -Δ wet season litter in fine - mesh bags

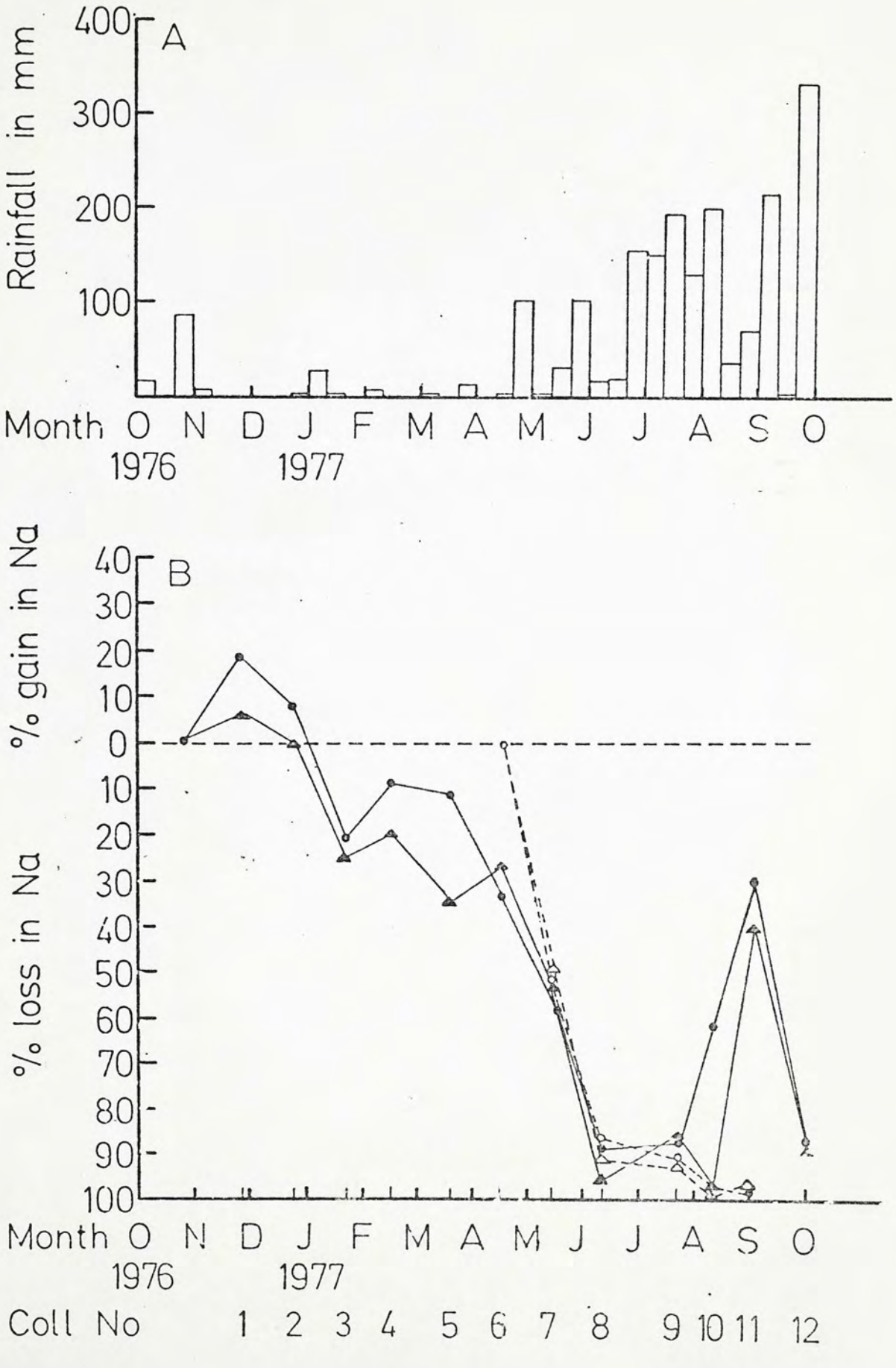

A
Rainfall in mm
400
300
200
100
Month O N D J F M A M J J A S O
1976 1977
B
% gain in Na
% loss in Na
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
Month O N D J F M A M J J A S O
1976 1977
Coll No 1 2 3 4 5 6 7 8 9 10 11 12

Figure 3.16 Percentage change in potassium content of litter samples set out in the dry and wet seasons.

(Percentage change is expressed with reference to the initial potassium content.)

o——o dry season litter in coarse - mesh bags
Δ——Δ dry season litter in fine - mesh bags
o- - -o wet season litter in coarse - mesh bags
Δ - - -Δ wet season litter in fine - mesh bags

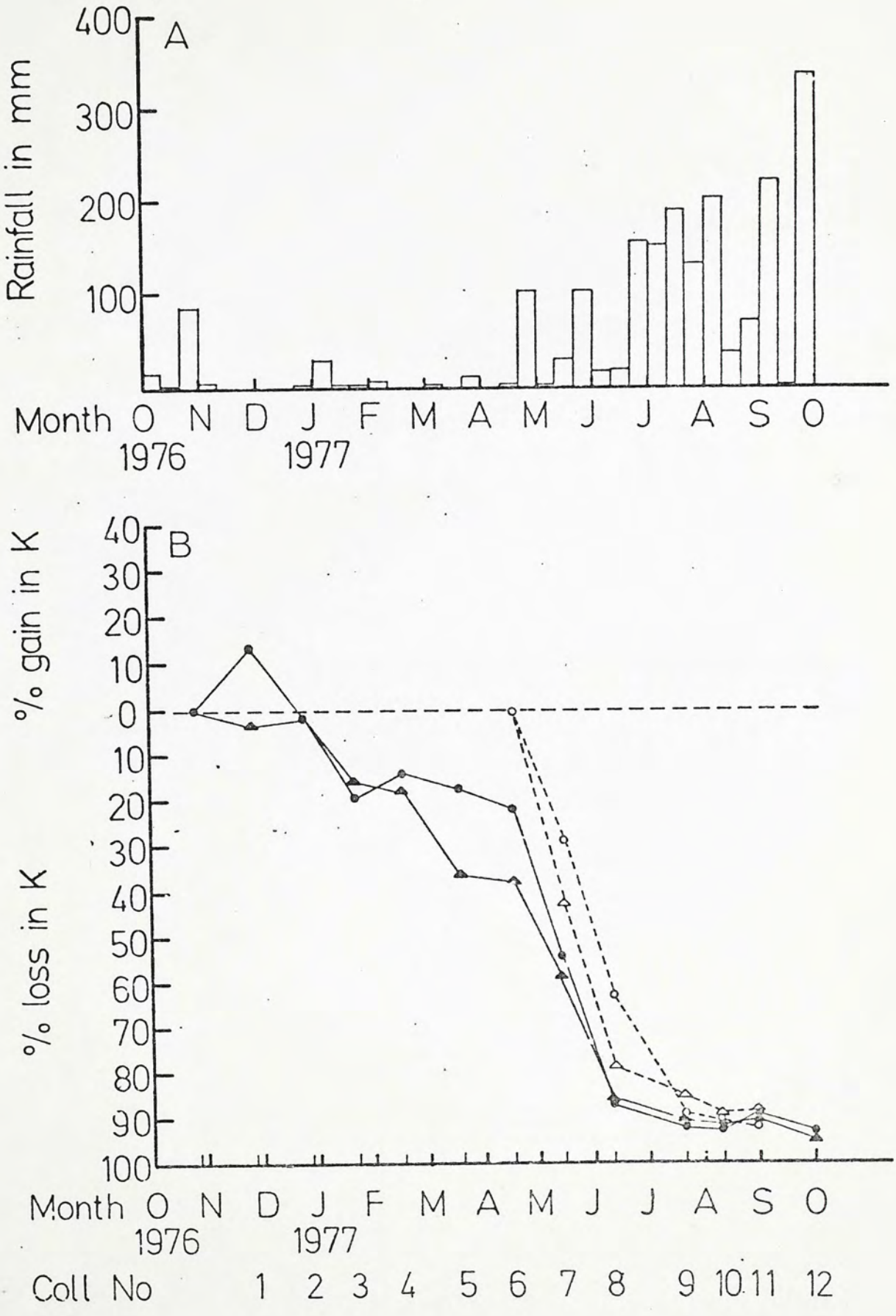

A
Rainfall in mm
400
300
200
100
Month O N D J F M A M J J A S O
1976 1977
B
% gain in K
% loss in K
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
Month O N D J F M A M J J A S O
1976 1977
Coll No 1 2 3 4 5 6 7 8 9 10 11 12

Figure 3.17 Percentage change in magnesium content of litter samples set out in the dry and wet seasons.

(Percentage change is expressed with reference to the initial magnesium content.)

●——● dry season litter in coarse - mesh bags
▲——▲ dry season litter in fine - mesh bags
○- - -○ wet season litter in coarse - mesh bags
△- - -△ wet season litter in fine - mesh bags

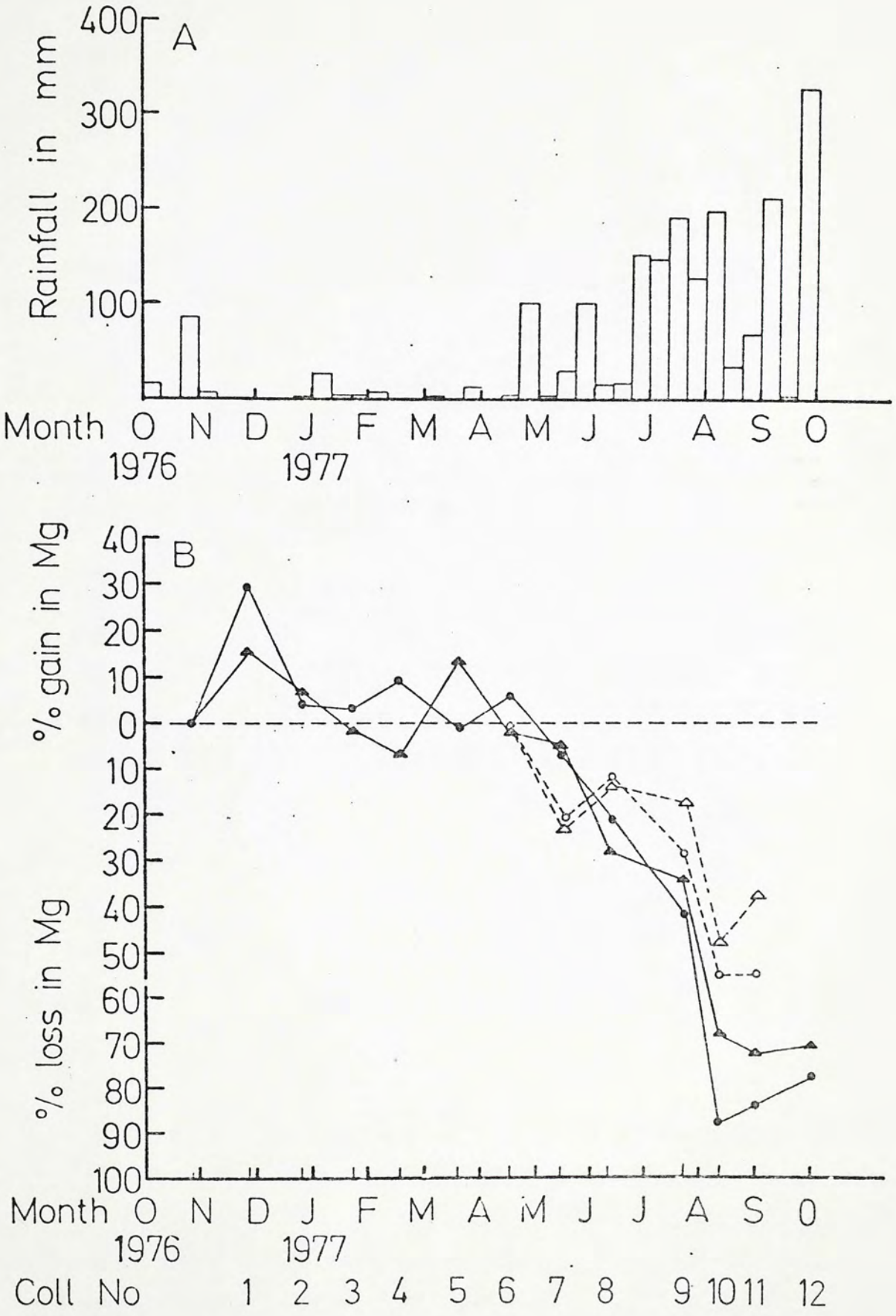
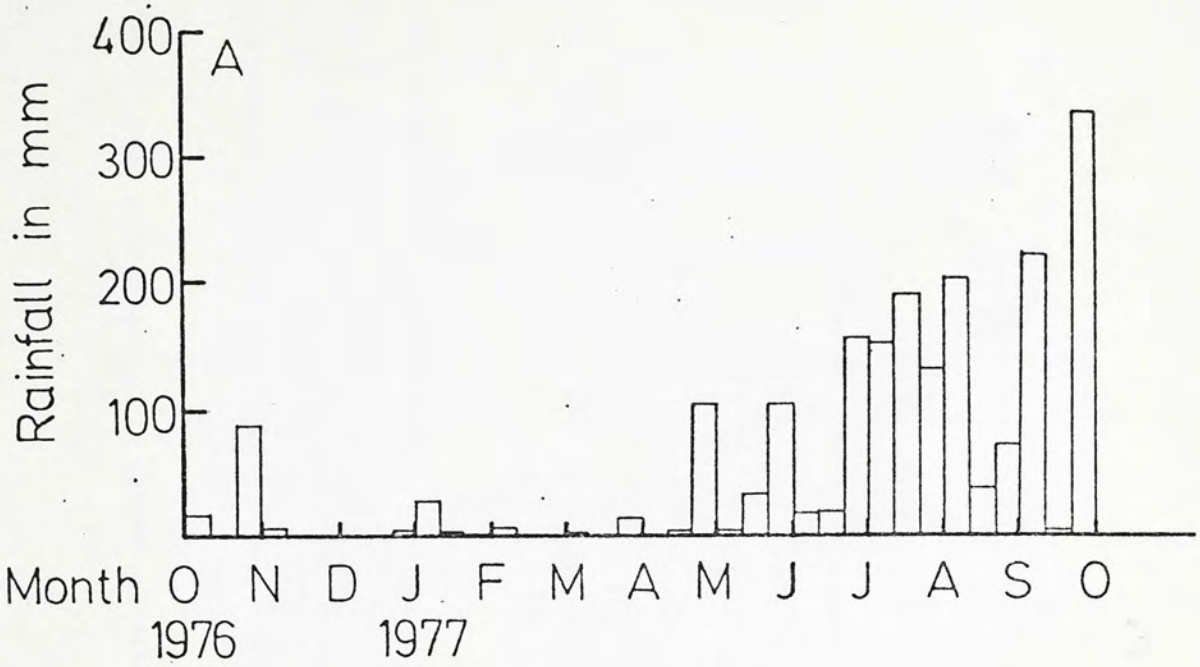

A
Rainfall in mm
400
300
200
100
Month O N D J F M A M J J A S O
1976 1977
B
% gain in Mg
% loss in Mg
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
Month O N D J F M A M J J A S O
1976 1977
Coll No 1 2 3 4 5 6 7 8 9 10 11 12

Figure 3.18 Percentage change in calcium content of litter samples set out in the dry and wet seasons.

(Percentage change is expressed with reference to the initial calcium content.)

●——● dry season litter in coarse - mesh bags
▲——▲ dry season litter in fine - mesh bags
○- - -○ wet season litter in coarse - mesh bags
△- - -△ wet season litter in fine - mesh bags


A
Rainfall in mm
400
300
200
100
Month O N D J F M A M J J A S O
1976
1977

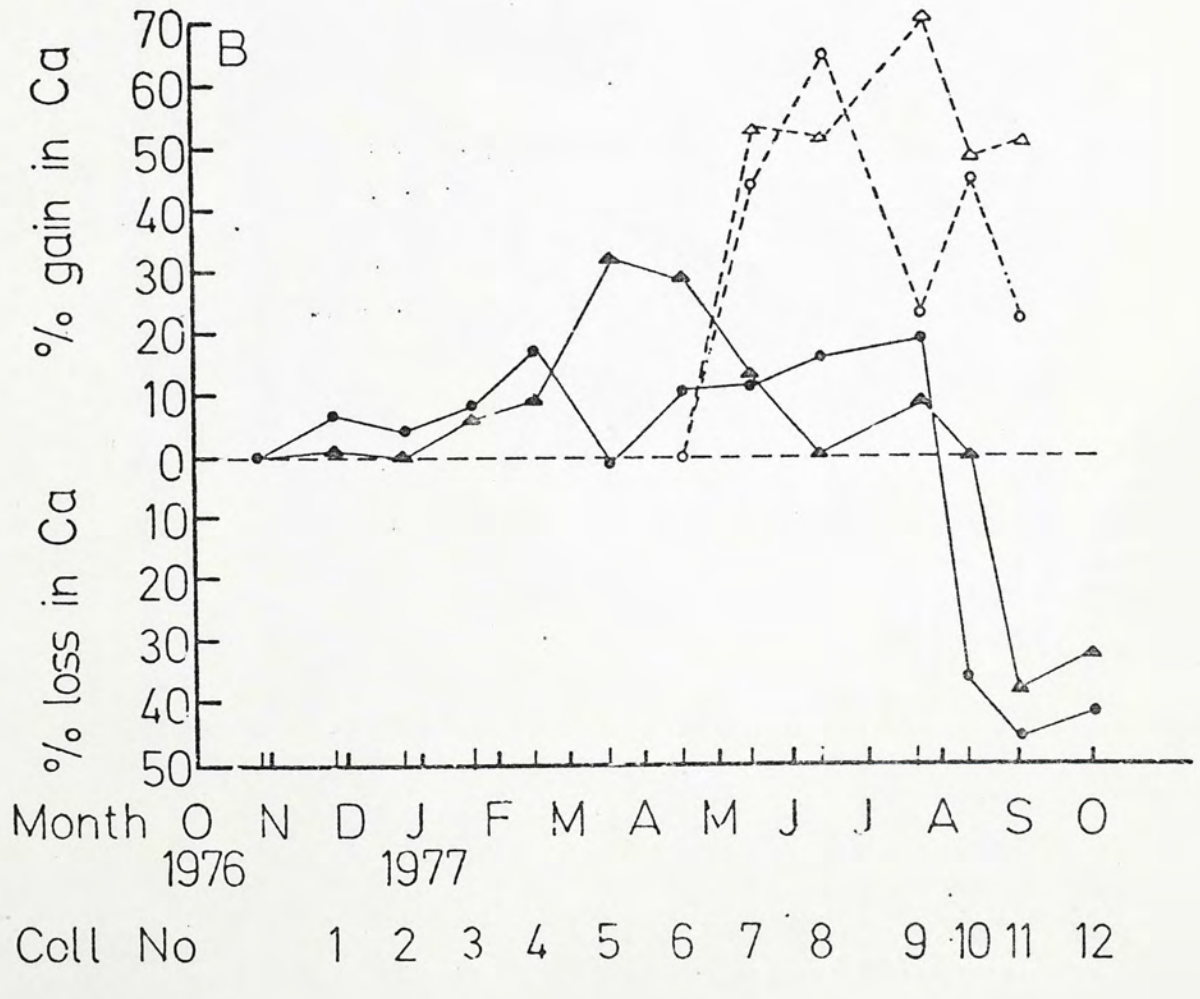

B
% gain in Ca
% loss in Ca
70
60
50
40
30
20
10
0
10
20
30
40
50
Month O N D J F M A M J J A S O
1976
1977
Coll No 1 2 3 4 5 6 7 8 9 10 11 12

Table 3.1 'The dry weight at collection, percentage loss in dry weight and percentage moisture of litter samples from coarse and fine-mesh bags set out in the dry and the wet seasons.

Date of collection	Rainfall (mm) for previous 28 days	Coarse Mesh				Fine Mesh			
		Dry wt at collection (g)	% loss in dry wt	% moisture on field wt basis	% moisture on dry wt basis	Dry wt at collection (g)	% loss in dry wt	% moisture on field wt basis	% moisture on dry wt basis
Dry Season									
1976. 26 Nov	30.7	5.15	-	13.82	16.04	5.10	-	13.82	16.04
23 Dec	0	4.99	0.21	19.43	24.11	5.05	-	19.54	24.29
1977. 20 Jan	28.9	5.16	-	21.87	28.00	4.96	0.80	23.88	31.37
15 Feb	5.9	5.11	-	12.74	14.61	5.07	-	13.47	15.57
17 Mar	2.9	4.83	3.27	16.13	19.23	4.55	9.83	14.63	17.14
14 Apr	16.1	4.98	4.7	19.36	24.00	4.61	5.23	18.80	23.15
12 May	106.1	4.45	10.13	16.44	19.67	4.33.	13.42	19.20	23.76
9 Jun	151.9	3.64	27.17	61.18	157.62	7.02	-	31.20	45.35
19 Jul	348.4	3.38	28.91	35.35	54.67	3.74	25.05	34.32	52.25
10 Aug	464.8	3.13	37.28	70.70	241.25	3.25	35.53	70.29	236.62
1 Sep	128.4	2.53	49.35+	60.27	150.14	3.18	36.96	64.75	183.71
30 Sep	487.3	3.18	37.58	72.61	265.09	3.05	38.46	73.60	278.79
Wet Season									
1977. 12 May	106.1	5.10	5.54	13.23	15.24	5.20	4.52	14.17	16.54
9 Jun	151.9	4.36	24.04	51.03	104.20	4.28	20.42	56.68	130.86
19 Jul	348.4	3.65	33.23	48.21	93.09	3.62	33.11	53.96	117.20
10 Aug	464.8	3.82	30.50	68.99	222.48	3.83	29.70	70.33	237.04
1 Sep	126.4	3.30	38.92	52.93	112.46	3.53	36.60	57.14	133.32

+ loss of fragmented samples

• heavily contaminated with soil

Table 3.2 The cation content[@] (mg/g) of fresh senescent leaves from the same stand of Rhodomyrtus tomentosa as the initial leaf samples.

Date of collection	Rainfall (mm) for previous 28 days	Sodium	Potassium	Magnesium	Calcium
1976. 25 Oct	-	0.57	8.00	1.07	3.43
26 Nov	30.7	-	-	-	-
23 Dec	0	-	-	-	-
1977. 20 Jan	28.9	0.46	7.56	1.08	3.47
15 Feb	5.9	0.58	8.42	1.03	3.51
17 Mar	2.9	0.39	7.55	1.08	4.06
14 Apr	16.1	0.45	5.37	0.93	3.11
12 May	106.1	0.46	5.12	1.22	4.58
9 Jun	151.9	-	-	-	-
19 Jul	348.4	0.57	6.80	1.15	4.10
10 Aug	464.8	0.49	6.02	1.07	3.69
1 Sep	128.4	0.60	5.70	1.03	3.65
30 Sep	487.3	0.62	5.75	1.03	4.68

[@]The cation content is expressed with reference to the dry weight of the fresh senescent leaves at the time of collection.

Table 3.3 The cation content[@] (mg/g) of litter samples from coarse and fine-mesh bags set out in the dry and wet seasons.

Date of collection	Rainfall (mm) for previous 28 days	Coarse Mesh				Fine Mesh			
		Sodium	Potassium	Magnesium	Calcium	Sodium	Potassium	Magnesium	Calcium
Dry Season 1976. 25 Oct (control)	-	0.57	8.00	1.06	3.43	0.57	8.00	1.06	3.43
26 Nov	30.7	0.69	9.07	1.38	3.65	0.61	7.76	1.18	3.47
23 Dec	0	0.62	7.85	1.11	3.58	0.57	7.83	1.14	3.44
1977. 20 Jan	28.9	0.45	6.47	1.10	3.71	0.43	6.73	1.05	3.66
15 Feb	5.9	0.52	6.89	1.17	4.03	0.46	6.63	0.99	3.76
17 Mar	2.9	0.51	6.62	1.06	3.40	0.38	5.18	1.21	4.54
14 Apr	16.1	0.38	6.26	1.13	3.79	0.42	5.03	1.05	4.44
12 May	106.1	0.24	3.68	0.99	3.83	0.27	3.35	1.02	3.90
9 Jun	151.9	0.06	1.08	0.84	3.98	0.02	1.05	0.77	3.47
19 Jul	348.4	0.07	0.60	0.62	4.09	0.08	0.75	0.70	3.75
10 Aug	464.8	0.22	0.57	0.13	2.21	0.02*	0.61	0.34	3.45
1 Sep	128.4	0.40	0.81	0.17	1.86	0.35	0.79	0.30	2.14
30 Sep	487.3	0.07	0.55	0.24	2.02	0.07	0.51	0.32	2.34
Wet Season 1977. 24 Mar (control)	-	0.66	6.91	1.17	2.67	0.66	6.91	1.17	2.67
12 May	106.1	0.32	4.95	0.93	3.86	0.33	3.98	0.93	4.09
9 Jun	151.9	0.09	2.59	1.03	4.42	0.05	1.49	1.03	4.04
19 Jul	348.4	0.06	0.77	0.84	3.56	0.06	1.02	0.97	4.57
10 Aug	464.8	0.02	0.61	0.52	3.88	0.02	0.76	0.61	3.96
1 Sep	128.4	0.01	0.60	0.53	3.27	0.03	0.67	0.73	4.03

@ The cation content is expressed with reference to the dry weight of the litter samples at the time of collection.

* Data from one determination only , all others are from duplicate determinations.

CHAPTER 4

LITTER DECOMPOSITION: SUCCESSION OF THE MYCOFLORA

Leaves on living plants have their own mycoflora even when still in the bud stage, and this has been recognised in a spatial terminology; the "phyllosphere" and "phylloplane". The term phylloplane was adopted from the term phyllosphere which was first proposed by Last (1955) and Ruinen (1956) by analogy to the term 'rhizosphere'. Phyllosphere denotes the leaf surface and the immediately adjacent areas, while phylloplane denotes the actual surface of the leaf (Tarr, 1972). Smit and Wieringa (1953) were early workers on the saprophytic fungi of the phylloplane, and they reported that Aureobasidium pullulans occurred regularly on the leaves of many different deciduous trees and shrubs. Similarly, Aureobasidium pullulans has been isolated from leaves in bud (Pugh and Buckley, 1971b) as has Cladosporium herbarum (Keener, 1951). Aureobasidium pullulans and other fungi may occur in the active form in the phylloplane or they may remain as inactive forms until the leaf becomes senescent and falls. After the leaves have fallen to the ground, the leaf mycoflora may become active for a period of time. These fungi are joined by new colonizers from the litter layer as the process of decomposition begins. At later stages of decomposition, the intiial colonizers may disappear and their place be taken by typical soil fungi such as species of Penicillium, Trichoderma, Mucor and Mortierella (Hudson, 1968).

Much work has been done on fungal succession upon herbaceous litter, angiospermous and coniferous leaves and litter materials, and this has been extensively reviewed by Bell, Jensen and Millar (1974).

A number of methods have been used for the study of fungal populations on both the aerial parts of plants and on litter (Pugh, 1974). The techniques used since 1955 have been analysed by Lindsey (1973). The methods included isolation from dilution plates, from unwashed, washed or surface-sterilized litter, direct observation of development on litter incubated in moist chambers, and collection of spore deposits from litter suspended over nutrient agar plates (Jensen, 1974). Any one of these methods is insufficient in itself because each gives information only on certain sections of the fungal population. However, these methods are complementary to, and supplement, one another. A complete picture will eventually emerge by putting together information obtained by different techniques.

The purpose of the work described in this chapter was to study the pattern of fungal colonization and succession in relation to loss of dry weight and cations from the litter.

Materials and Method

The method of setting out leaf samples and their collection has been described in Chapter 3. The leaf samples for studying colonization by micro-organisms were processed immediately after collection; or if the circumstances did not allow immediate

processing, the samples were stored in a refrigerator (mean temperatuer 4°C) overnight and then processed.

a) Dry season litter samples

Leaves were taken at random from the bag with a mesh size of 1 mm (fine mesh). They were washed with seven changes of 1% Teepol solution, followed by eight changes of sterilized distilled water (Macauley and Thrower, 1966). Then each leaf was cut into two halves with sterilized scalpels. One half was cut into small pieces and plated on to Czapek-Dox agar and malt extract agar (Raper and Thom, 1949). The other half was surface-sterilized with 0.1 M mercuric chloride solution for 3 seconds, and then washed with sterilized distilled water. It was cut into pieces and plated out in the same way as the other half.

The plate cultures were allowed to grow at room temperature (26°C - 28°C) for one to two weeks depending on the rate and vigour of growth. The different species of fungi were isolated on to malt extract agar slants. The subcultures were examined and identified after sufficient growth was obtained. The guides to identification followed that of Ainsworth, Sparrow and Sussman (1973 a & b), von Arx (1957), Barnett (1955), Barron (1968), Chang (1963), Ellis (1971, 1976), Funder (1953), Gilman (1957), Guba (1961), Neergaard (1945), Raper and Thom (1949), Sawada (1959), Smith (1954), Thom and Raper (1945) and Zycha (1935).

b) Wet season litter samples

Litter samples set out at the beginning of the wet season were processed in the same way as litter samples set out in the dry season.

c) Control leaves

Senescent leaves freshly picked from the same stand of Rhodomyrtus tomentosa at each collection (control collections) were processed in the same way as the litter, so that a study of the fungal population on fresh senescent leaves could be made in relation to the season, and the mycofloras on the living leaves and litter could be compared.

d) Soil samples

A small sample of soil from beneath the litter bags was also gathered at each collection. The fungi in the sample of soil was isolated by the soil plate method (Warcup, 1950; Garrett, 1963), using the same media as for the litter and leaf samples.

Results

Growth in general was more diverse in Czapek-Dox agar than in malt extract agar. The latter allowed vigorous growth of fast-growing species. Therefore, the malt extract agar was not used for the latter half of the collections, and the results presented were based upon growth on Czapek-Dox agar. The frequency or abundance of occurrence of each species was expressed as the number of subcultures of the species divided by the total number of subcultures isolated for each collection, ie.,

$$\text{Frequency of a species} = \frac{\text{No. of subcultures of that species} \times 100}{\text{Total no. of subcultures}}$$

Separate calculations were made for surface colonizers and internal colonizers, and for each collection. This ratio reflected the frequency of occurrence fairly well since the number of subcultures isolated was proportional to the frequency and abundance of a species in each collection except in the case of Pestalotia sp. and Colletotrichum sp., in which only representative samples were isolated. Therefore, the fraction may under estimate the abundance of these two species.

The complete list of all fungi isolated from control leaves, litter samples in the dry and wet seasons, and surface soil from under the litter samples was given in Appendices 4.1, 4.2 and 4.3.

a) Fungi on fresh senescent leaves (control leaves)

The results are given in Table 4.1 as percentage frequency of the more important species.

(i) Surface colonizers

A number of species of Pestalotia such as Pestalotia langloisii and Pestalotia uvicola (Guba, 1961) were isolated; however, since the biology of leaf-inhabiting Pestalotia spp. is likely to be similar, the different species have been considered together. Pestalotia spp. (Figure 4.1) were found in nearly every control collection, and were sometimes contaminants of slow-growing subcultures on slopes of malt extract agar. The next important fungus was a greyish black mold, Phialophora fastigiata (Figure 4.2). It was specially frequent in control

collections during the rainy season. Sterile Species B also occurred regularly, its colonies were green and orange in color with numerous clear droplets on the surface (Figure 4.3). However, in culture it formed only swollen hyphae without any sign of spores (Figure 4.4). More than six "species" of Trichoderma occurred. When the frequency of all species was pooled, they reached a peak for control collection No. 8 (Appendix 4.1) at the beginning of the rainy season (June); pooling of the "species" seems acceptable in view of the widely-held opinion that all or most isolates of Trichoderma are referable to Trichoderma viride. Aspergillus niger (Figure 4.5) was seldom found in the dry season, but became important when the rainy season came. Other species which occurred regularly on living leaves included Penicillium sp. A, Fusarium spp., Curvularia spp. and Nigrospora sp. Nigrospora sp. was more frequently found on malt extract agar plates. Other species which occurred only occassionally are listed in Appendix 4.1.

(ii) Internal colonizers

Colletotrichum spp. were the most important colonizers in all the control collections. They grew more slowly than the surface fungi. In the first half of the control collections, Colletotrichum sp. A was more important (Figures 4.6 and 4.7), but in the latter

half, another species (Colletotrichum sp. B), whose growth was more floccose, became important (Figure 4.8); in the last two collections, it accounted for 67% and 91% respectively, of the total internal colonizers.

b) Fungi on the dry season litter

The results are given in Table 4.2 as the percentage frequency of the more important species.

(i) Surface colonizers

Important surface colonizers of the early collections of litter that had been set out in the dry season were Pestalotia spp. and Sterile Species B; these species were important on the control leaves. Fusarium sp. A (Figure 4.9) and Penicillium thomii (Figure 4.10) also occurred regularly on the early collections. Phialophora fastigiata was also abundant, reaching its peak in Collection No. 5, when it was co-dominant with Mucor hiemalis (Figure 4.11). Thereafter, these species began to decline in importance; all disappeared completely after Collection No. 8, except for Mucor hiemalis which became important again in Collection No. 10. Trichoderma spp. were recorded on early collections, but they first became important on Collection No. 6. Trichoderma glaucum (Figure 4.12) and Trichoderma viride (Figure 4.13) accounted for nearly 80% of the total subcultures on Collection

No. 7. Trichoderma viride was more frequent in the earlier collections, but at later collections it was replaced by Trichoderma koningii and other Trichodermas. Other species of Mucor besides Mucor hiemalis became important at later stages of decomposition, especially Mucor circinelloides (Figure 4.14) which was an important colonizer in the last collection (No. 12).

(ii) Internal colonizers

Colletotrichum sp. A was also an important internal colonizer of the litter samples set out in the dry season. However, it decreased in abundance and importance, and disappeared completely after Collection No. 8. Sterile Species D was also frequent in early collections, and decreased in importance as did Colletotrichum sp. A. The dominance of Colletotrichum sp. and Sterile Species D as internal colonizers was taken over by Phomopsis spp. in the latter half of the collections. Phomopsis sp A (Figure 4.15) occurred in nearly every collection but reached a peak of over 40% in Collection No. 8. Phomopsis psidii (Figure 4.16) was fairly important throughout, and reached its peak abundance in Collection No. 10. The internal colonizers grew very slowly or not at all from leaf tissue in the last two collections, and only a very few sterile subcultures were obtained.

c) Fungi on the wet season litter

The results are given in Table 4.3 as the percentage frequency of the more important species.

(i) Surface colonizers

The surface colonizers found on the litter set out at the beginning of the wet season were comparable to those on the litter set out at the beginning of the dry season. Pestalotia spp. were present on the first two collections but then disappeared. Fusarium oxysporum and Fusarium sp. A were fairly important throughout. Mucor circinelloides and Mucor hiemalis were important in the later stages. Trichoderma spp. pooled together were the dominant colonizers of the last two collections.

(ii) Internal colonizers

As in the control collections and the dry-season set of litter samples, Colletotrichum sp. A was an important early internal colonizer. However, the diversity of species which were dominant internal colonizers was greater than either of the previous two sets of leaves. Phomopsis sp. A occurred in co-dominance with Colletotrichum sp. A up to Collection No. 3W, when another species, Scolecobasidium humicola (Figure 4.17), shared the co-dominance. Beltraniella nilgirica was the most important colonizer of Collection No. 4W, and Parasympodiella laxa of Collection No. 5W (Figure 4.18).

d) Soil mycoflora

The results are given in Table 4.4 as percentage frequency of the more important species.

The soil mycoflora was relatively simple, probably because the dominant species were fast growing. Penicillium sp. Penicillium thomii and Penicillium wortmanii (Figures 4.10 and 4.19) occurred throughout the collections. Trichoderma viride was very abundant in the first two collections, and was again important in Collection No. 8. Trichoderma hamatum was abundant in Collection No. 7. Trichoderma koningii was also fairly frequent. Neurospora crassa and Phialomyces macrosporus were found occassionally among the soil mycoflora; Neurospora crassa was possibly a contaminant due to wind-blown conidia being carried from burnt vegetation on which this species sporulates abundantly. Mucor spp. were seldom found, although they have been reported to be prevalent in the lower layers of litter (Saito, 1966).

Penicillium wortmanii and species of Trichoderma were important in surface soil beneath the wet season litter in the same way as beneath the dry season litter.

e) Mites and nematodes associated with the litter samples

Mites were found associated with litter samples collected at the beginning of the wet season. Their eggs were laid on the litter surface and, when pieces of litter were washed and plated, the eggs hatched on the culture medium. The mites were species of Tyrophagus (Figure 4.20), and they

were found mostly in association with the black mold Phialophora fastigiata. They were most abundant in Collections Nos. 7, 8 and 9 in the dry-season set of litter and Nos. 2W, 3W and 4W in the wet-season set (the time of collection of these samples in the two sets coincided). Mites were found less frequently in litter samples sterilized with mercuric chloride solution, probably because their eggs were killed. Nematodes existed concurrently with the mites (Figure 4.21). However, when the number of mites declined gradually on successive collections they were succeeded by nematodes entirely, which consumed all mycelia when a suitable amount had grown. The nematodes were especially abundant in the wet season and the number reached a peak in the last collection of the dry-season set (ie. in the month of September which occurs in the wet season). They seemed to prefer Mucor sp. as their food.

Discussion

Leaves of the living plant had a mycoflora of their own. The mycoflora was fairly diverse, but a few species were common with the soil mycoflora. The leaf mycoflora was inactive when the environmental conditions were favorable for plant growth and the leaves were in a healthy condition. After the leaves became senescent and fell to the ground, their mycoflora became active. As observed in litter samples set out in the dry season, these species were dominant for the first few months of decomposition, but were gradually replaced by Mucor spp. and

Trichoderma spp., which are common soil fungi. There was an interesting interaction between members of these two genera as surface colonizers of leaves put out in the dry season (Figure 4.22 B). These fungi were present together in Collection No. 3 and, in the next two collections Trichoderma decreased while Mucor increased. Only Trichoderma was present on Collection No. 7. Thereafter Mucor increased (except for Collection No. 11) and became the dominant surface colonizer in Collection No. 12. Mucor spp., especially Mucor hiemalis, were considered as secondary sugar fungi on deciduous and coniferous litter (Hogg and Hudson, 1966; Kendrick and Burges, 1962). They colonized substrates in association with cellulolytic and perhaps lignin-decomposing fungi. They would not appear as primary colonizers as they do on coprophilous substrates which are high in carbohydrate content. Therefore it was possible in the present study that Trichoderma spp. decomposed the cellullose, and the products became available to the Mucor spp.; this would account for the change in abundance of Trichoderma spp. and Mucor spp. as decomposition progressed. Thus a succession was clearly seen from a more diverse mycoflora to a simpler one with few important species. On litter samples set out in the wet season, Mucor spp. were important in the third collection. However, Trichoderma spp. became more important in the fourth and fifth collections. On the basis of the interaction between Mucor spp. and Trichoderma spp. in the dry-season litter, the peak abundance of Trichoderma was

expected to be followed by peak abundance of Mucor in the samples set out in the wet season, which mycoflora resembled the later stage of the dry-season set. This was probably the effect of seasonal factors which shortened the time of decomposition. The most important factor may be the high moisture level, which is concomitant with higher temperature in the wet season.

The sequence of change in the composition and relative abundance of mycoflora was not only a succession due to change of substrate accompanying decomposition, but also a succession through the seasons as Moeller has suggested (1965). For example, Trichoderma became more active when the wet season came: its peak activity was observed not only in litter samples (Collection No. 7) but also on control leaves. Seasonality was also observed in Phialophora fastigiata which occurred on both fresh senescent leaves and litter samples. It showed peak abundance at the beginning of the wet season (Collection No. 5), but declined thereafter. On the other hand, there was a clear succession in the litter samples set out in the dry season, which was not shared by control leaves. Important indicator species such as Mucor sp. were seldom found on control leaves. By contrast, species such as Alternaria sp., Curvularia sp. and Nigrospora sp. were never found on litter samples. Succession could easily be envisaged in the litter since the physical and chemical properties of litter was continuously changing (Strenzke, 1963) creating differing micro-environments. However, conditions on leaves of the living plant were more or less constant, and this was

reflected by the regular occurrence of certain species. In this case the major factor causing any change in the mycoflora of control leaves is a seasonal succession, the change in the litter samples is a decompositional succession which was influenced to a great extent by the effect of season.

The internal colonizers Colletotrichum and Phomopsis were good indicators of successional change during decomposition. Whereas external colonization had involved Trichoderma and Mucor, internal colonization of the leaves put out in the dry season was essentially an interaction between Colletotrichum spp. and Phomopsis spp. (Figure 4.22 C). At the beginning of decomposition, Colletotrichum was very abundant while Phomopsis was essentially absent. While Colletotrichum fluctuated and declined slowly as decomposition progressed, Phomopsis increased steadily. At the point when Colletotrichum had almost disappeared, Phomopsis reached a peak of abundance, and thereafter its abundance was maintained at a steady high level. Internal colonization also showed a clear succession in the leaves put out in the wet season, and species occurring in the later collections (which were in an advanced stage of decay) were not found at all in the control leaves.

It might be expected that a succession of internal colonizers (if it occurred at all) would be a more clear-cut process than in the case of surface colonizers because casual contamination by conidia would be less likely. The results in Figure 4.22 conform to this expetation.

The change in the fauna (mites and nematodes) also showed a succession which was a result of both decomposition and season. As the litter became progressively fragmented, the moisture content increased, which favored most soil micro-fauna. Possibly mites visited the litter early in the decomposition process, and their eggs hatched when favorable warm and moist conditions came. The condition in the wet season also favored colonization by nematodes. The determining environmental factors were temperature, moisture and food supply (Twinn, 1974). Nematodes may be bacterivores or fungivores, which show sequential change in abundance as decomposition progresses. Studies by Twinn (1962) and Waid (1960) showed a close correspondence between the colonization by fungi and by the fungivorous nematodes. In the present study nematodes favored particularly the Mucorales, probably because the tall growth habit offered good aeration. The observation that both mites and nematodes were found associated with fungal subcultures pointed up the complexity of the decomposition process.

A wide variety of fungal species has been recorded from both fresh leaves and litter by a number of workers. Although each species of plant has its distinct leaf and litter mycoflora, many of the fungal colonizers are common. Genera found on fresh leaves in the present study, such as Pestalotia, Alternaria, Nigrospora, Trichoderma, Fusarium and Curvularia, have been recorded in other studies (Hudson, 1968; Norse, 1972a & b; Pugh and Williams, 1968; Ruscoe, 1971). Genera on litter, such

as Trichoderma, Mucor and Penicillium, are also common with those recorded in most other studies.

A number of species of other fungi were very common. Aureobasidium pullulans, Cladosporium herbarum, Epicoccum sp., Alternaria sp. and Botrytis sp. were found on leaves of Acer pseudoplatanus (Pugh and Buckley, 1971a), Beta sp. (Kerling, 1958), Fagus sylvatica (Hogg and Hudson, 1966), and Urtica dioica (Yadav and Madelin, 1968a). Aureobasidium pullulans and Cladosporium sp. were also found on litter of Fagus sylvatica (Hogg and Hudson, 1966), mixed oak-wood (Hering, 1965), mixed maple-elm-ash forest (Novak and Wittingham, 1968), mixed Quercus stand (Remacle, 1970 and 1971), Nothofagus truncata (Ruscoe, 1971), and Quercus robur (Witkamp, 1960). Species of Mucor, Trichoderma, Penicillium and Mortierella were found on older litter of Eucalyptus regnans (Macauley and Thrower, 1966), Fagus crenata (Saito, 1966), Juncus squarrosus (Latter and Cragg, 1967), Quercus robur (Witkamp, 1960) and on pine needles (Ward, 1952; Bransberg, 1969).

By integrating information from various sources,a general pattern of fungal succession on litter can be visualized. There are three stages in the successional change. During the first stage, the litter mycoflora was essentially the original leaf mycoflora, ie. the inhabitants of the phylloplane. This was gradually replaced by litter-decomposing fungi. Finally, as the litter became incorporated progressively into the soil, the litter decomposers were displaced by a soil mycoflora. However,

the transition from one to another took place gradually, and the time taken for the change differed for litter placed in different environmental conditions. The effect of season, especially moisture level, was most important in determining the frequency and abundance of species present and the rate of decomposition.

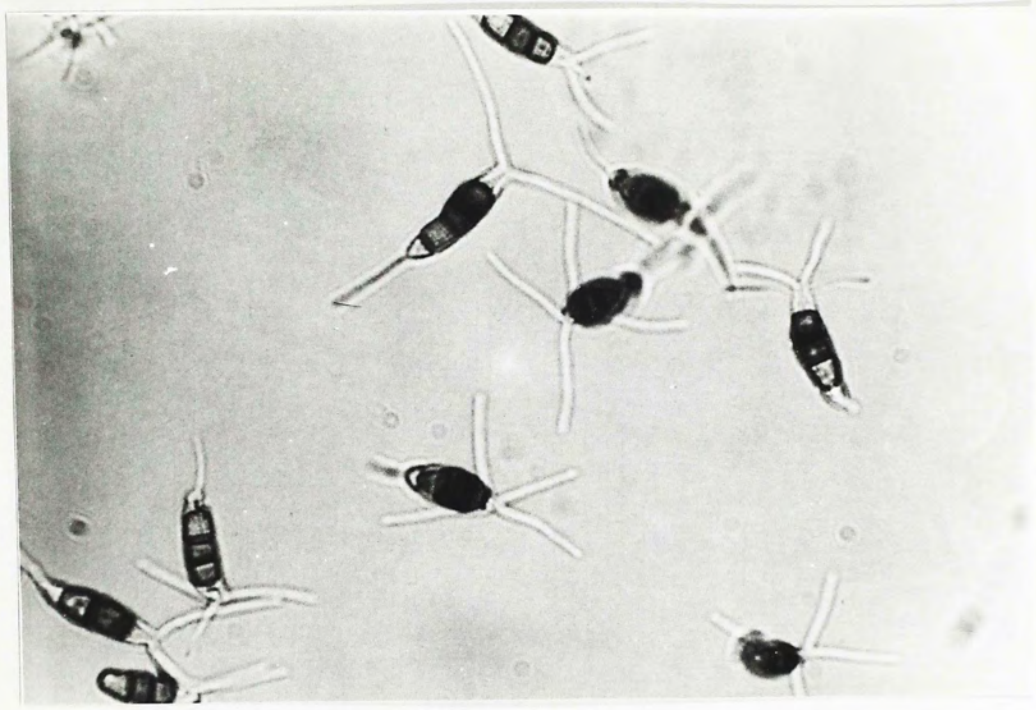


Figure 4.1 Pestalotia sp. : condia
(average length of condia excluding setae
= 25.4 µm).

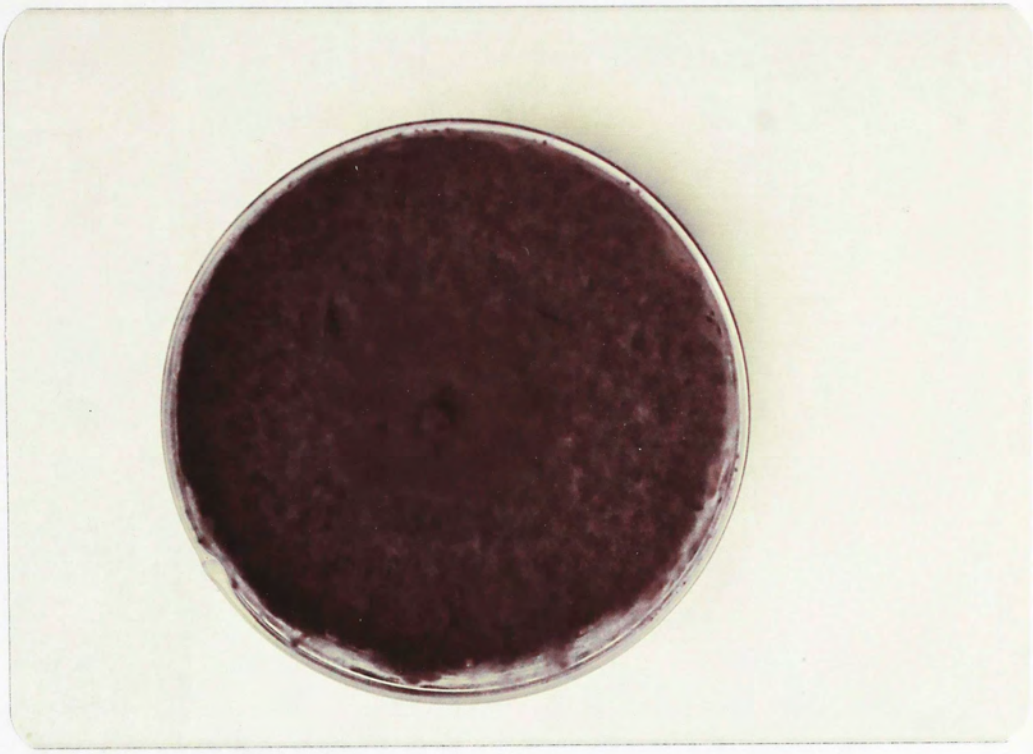


Figure 4.2 *Phialophora fastigiata* on malt extract agar.

Figure 4.3 Sterile species B on malt extract agar.

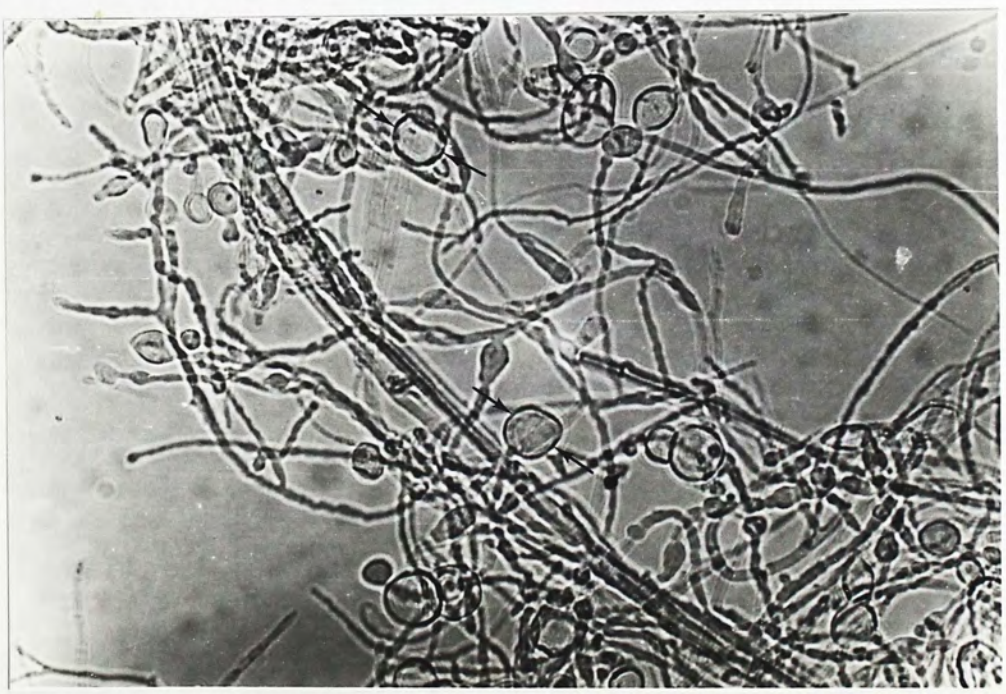


Figure 4.4 Sterile species B : habit showing swollen hyphae.
(average diameter of swollen hyphae = 25.4 µm).

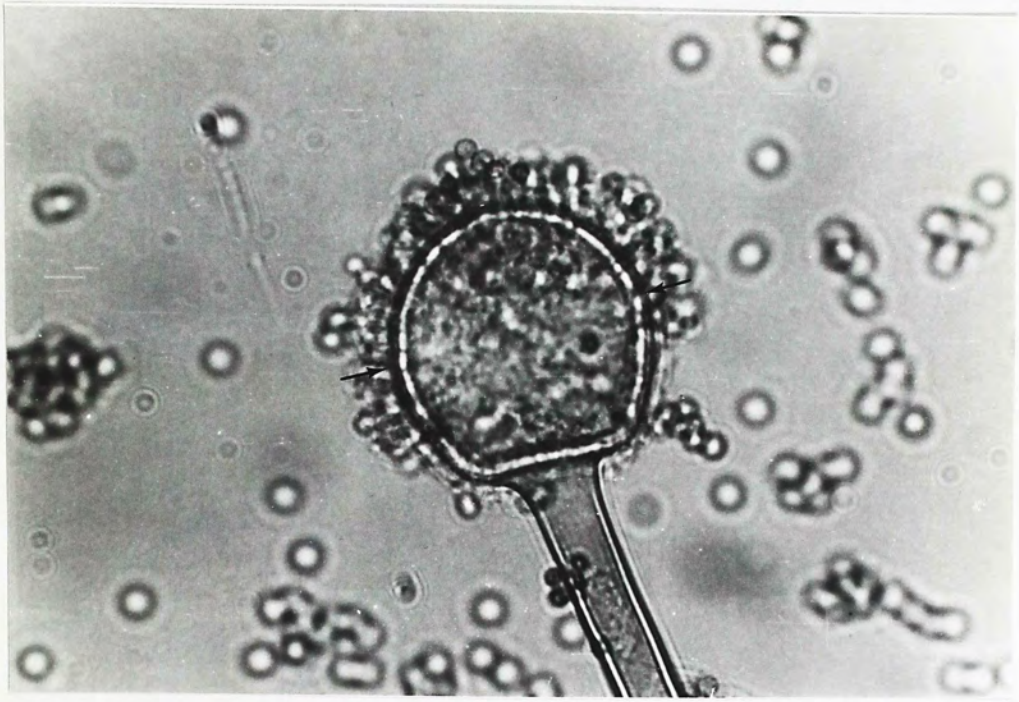


Figure 4.5 Aspergillus niger
(diameter of vesicle = 44.6 μ m).

Figure 4.6 Colletotrichum sp. A on Czapek-Dox agar

Figure 4.7 Colletotrichum sp. A : condia
(average length of condia = 12.7 μm).

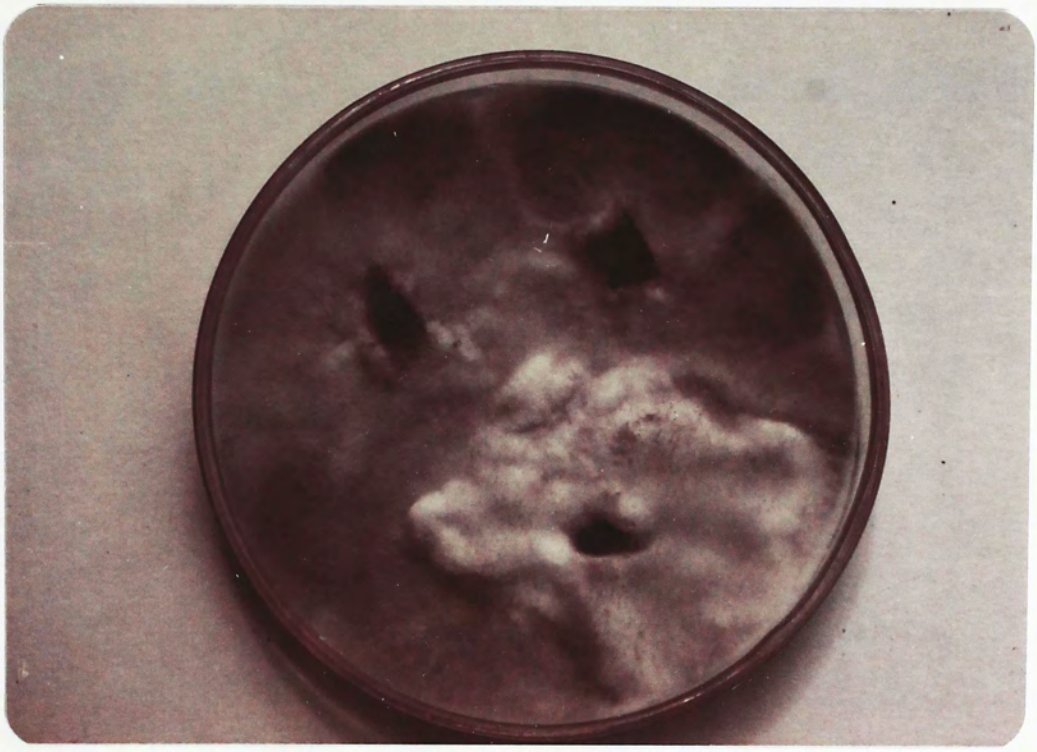


Figure 4.8 Colletotrichum sp. B on Czapek-Dox agar.

Figure 4.9 Fusarium sp. A : condia
(average length of conidia = 19.4 µm).

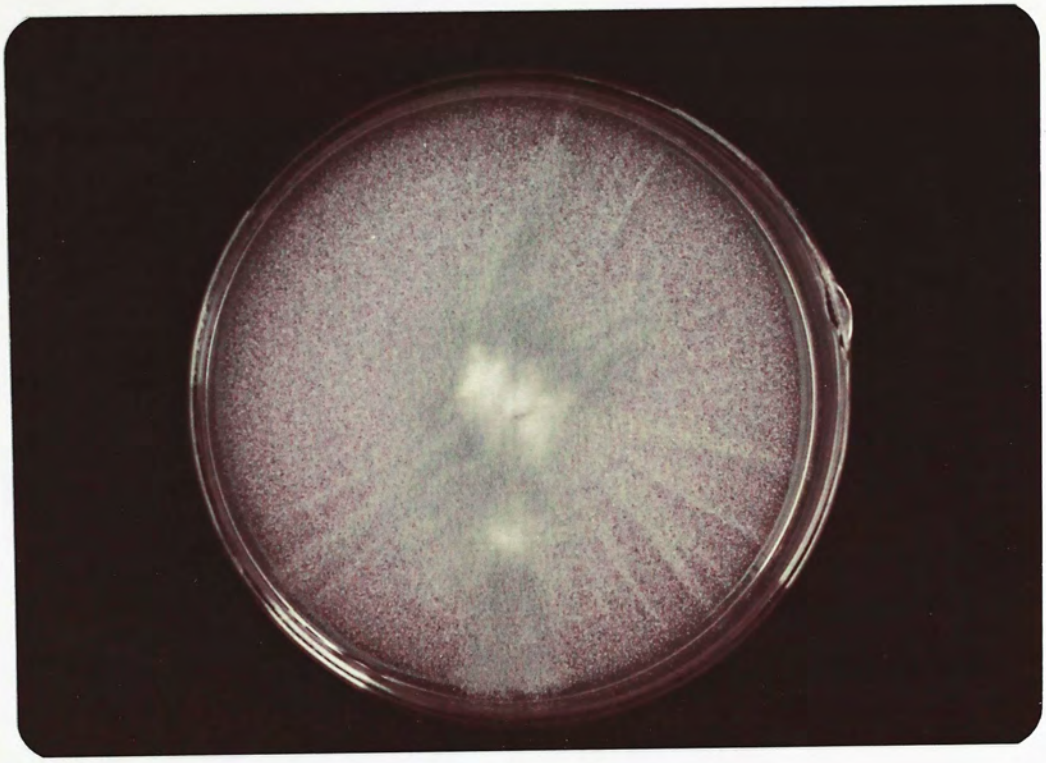


Figure 4.10 Penicillium thomii on malt extract agar.

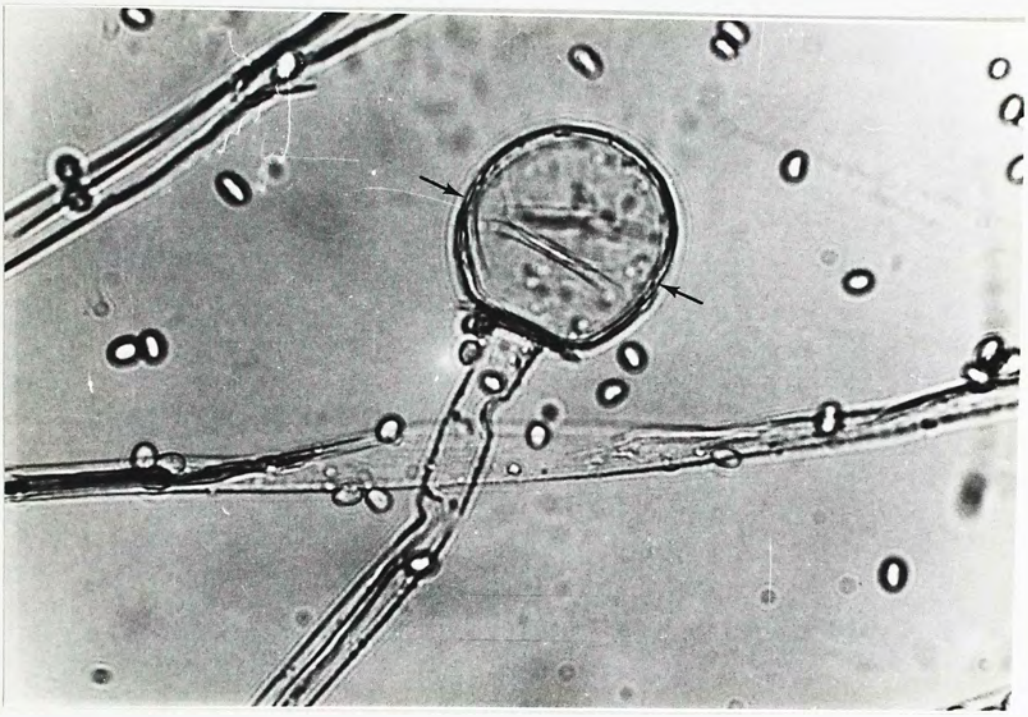


Figure 4.11 Mucor hiemalis
(diameter of collumella = 38.1 µm).

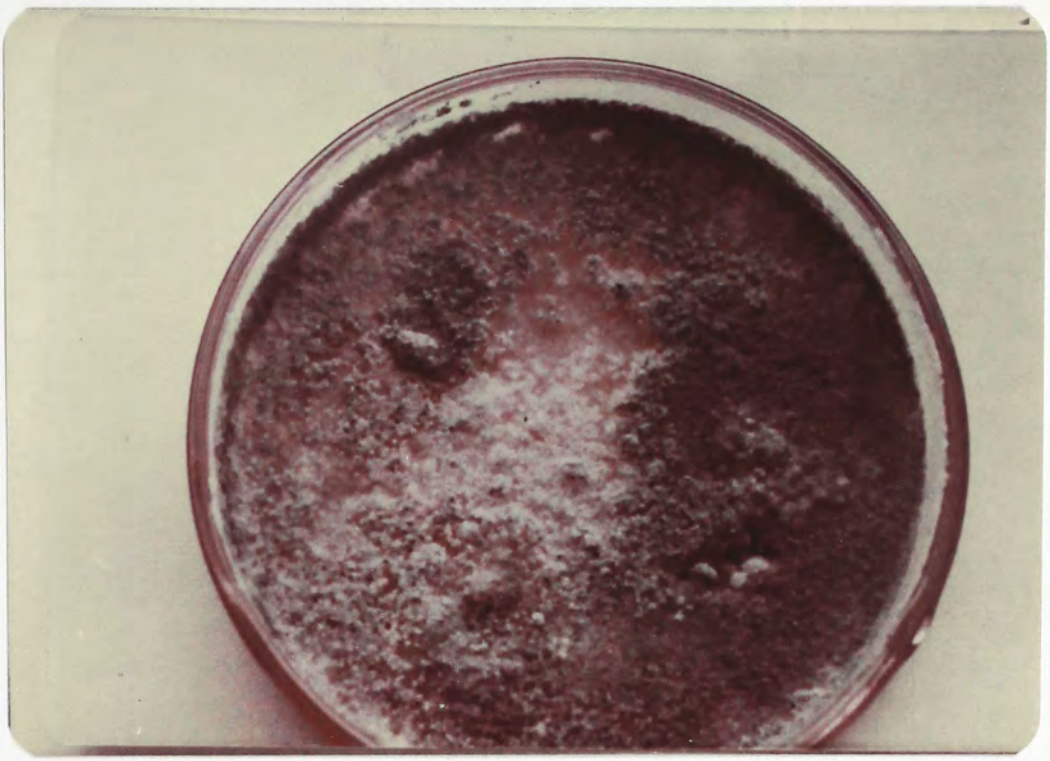


Figure 4.12 Trichoderma glaucum on Czapek-Dox agar.

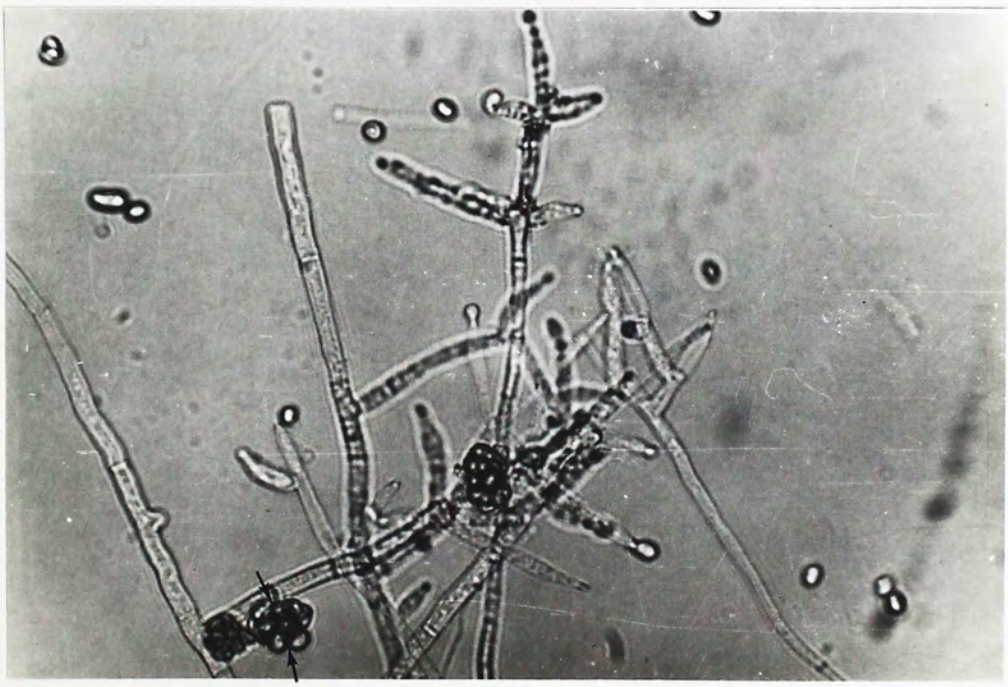


Figure 4.13 Trichoderma viride : habit
(diameter of the cluster of spores = 12.7 μm).

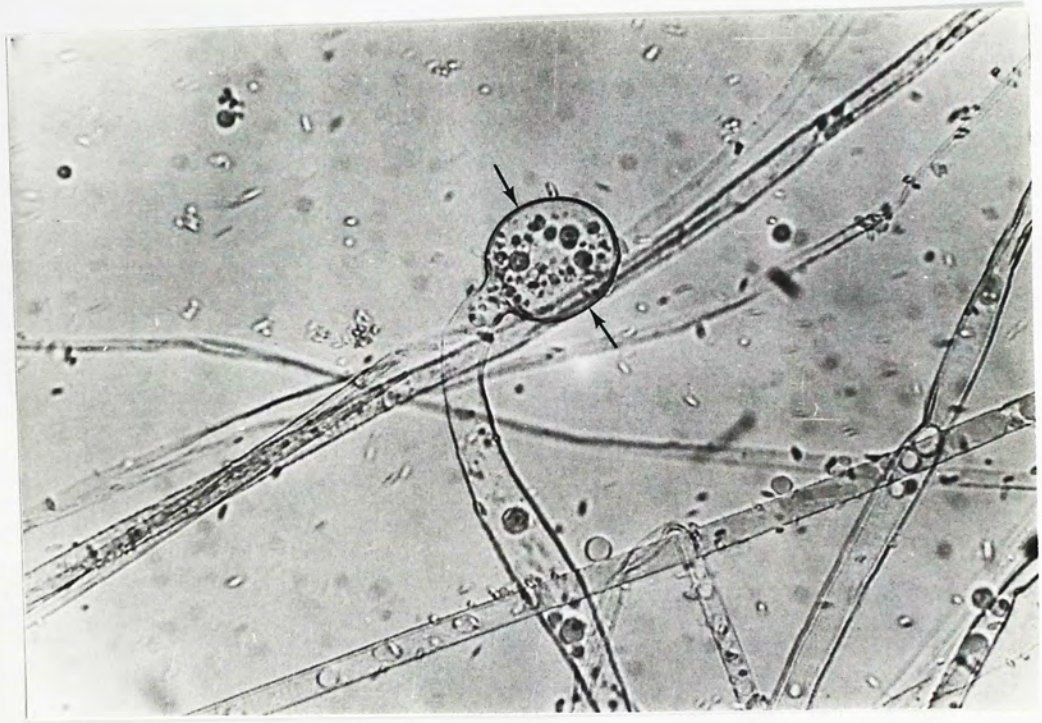


Figure 4.14 Mucor circinelloides
(diameter of collumella = 38.8 μm).

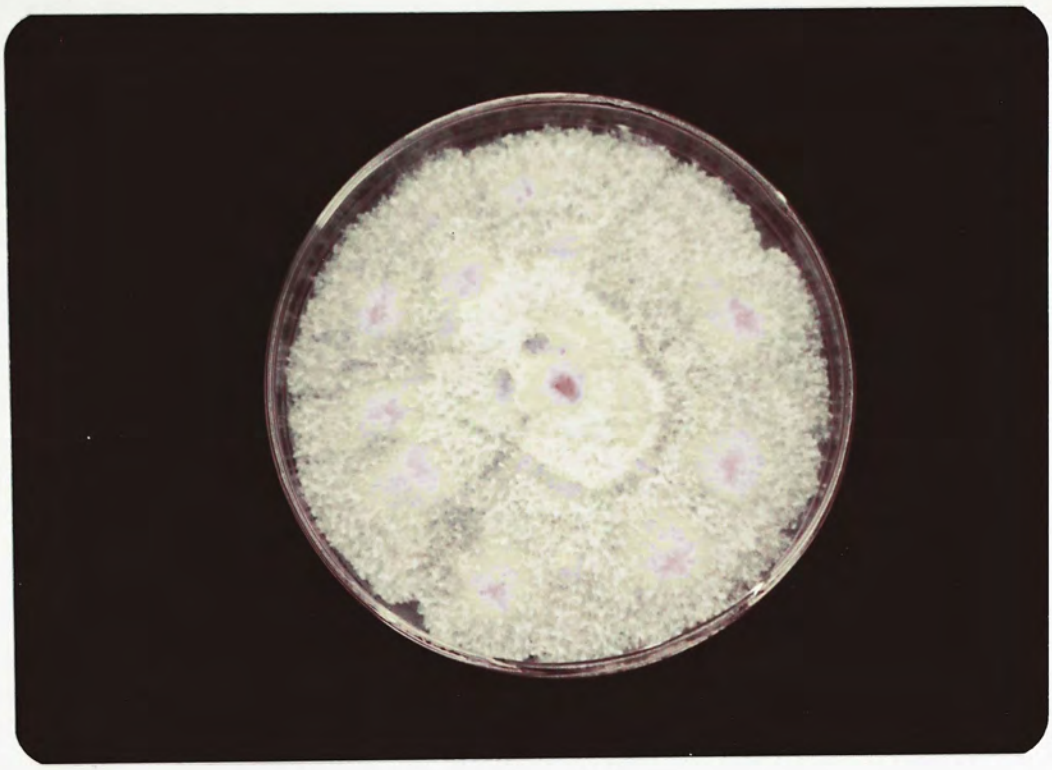


Figure 4.15 Phomopsis sp. A on malt extract agar.

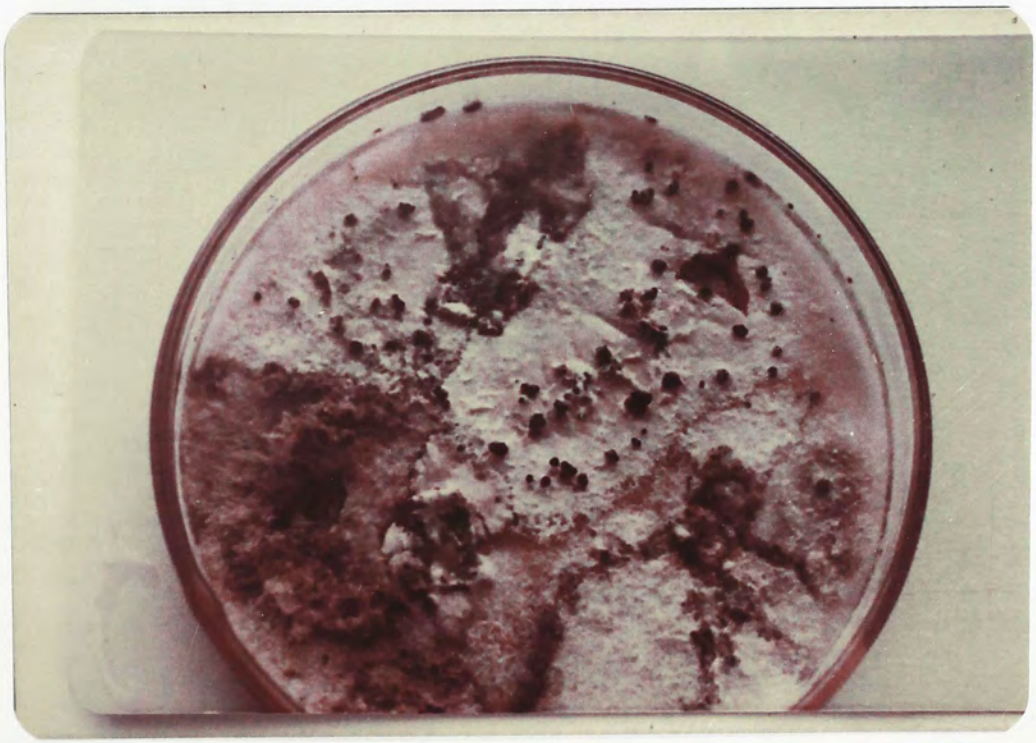


Figure 4.16 Phomopsis psidii on Czapek-Dox agar.

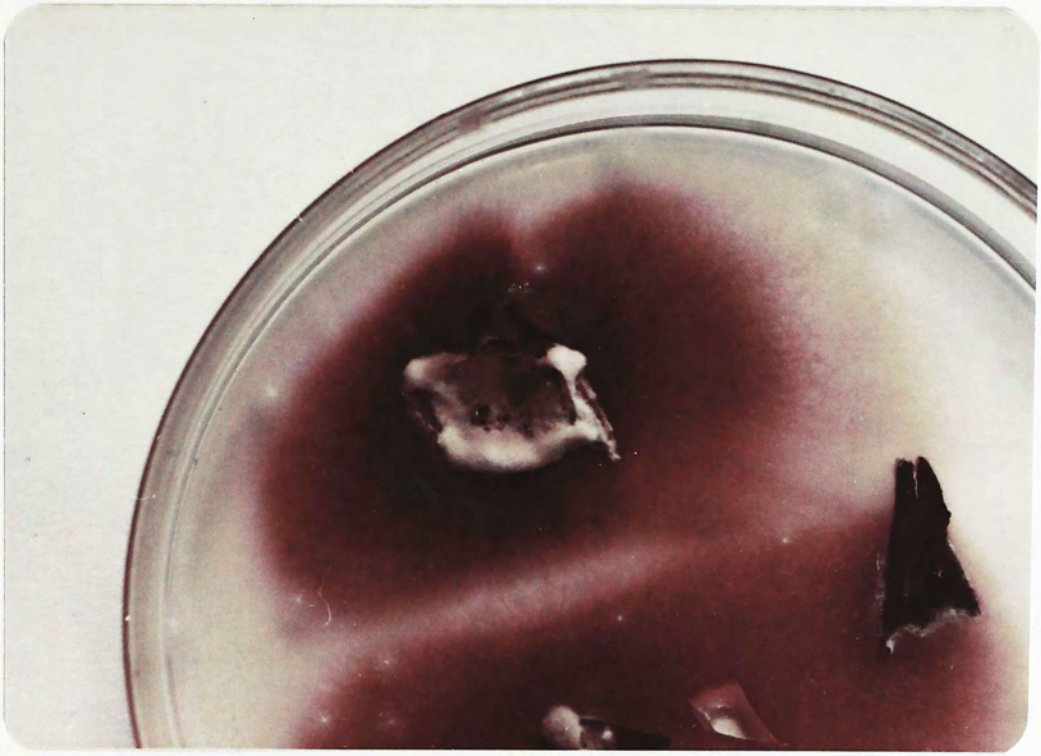


Figure 4.17 Scolecobasidium humicola on Czapek-Dox agar.

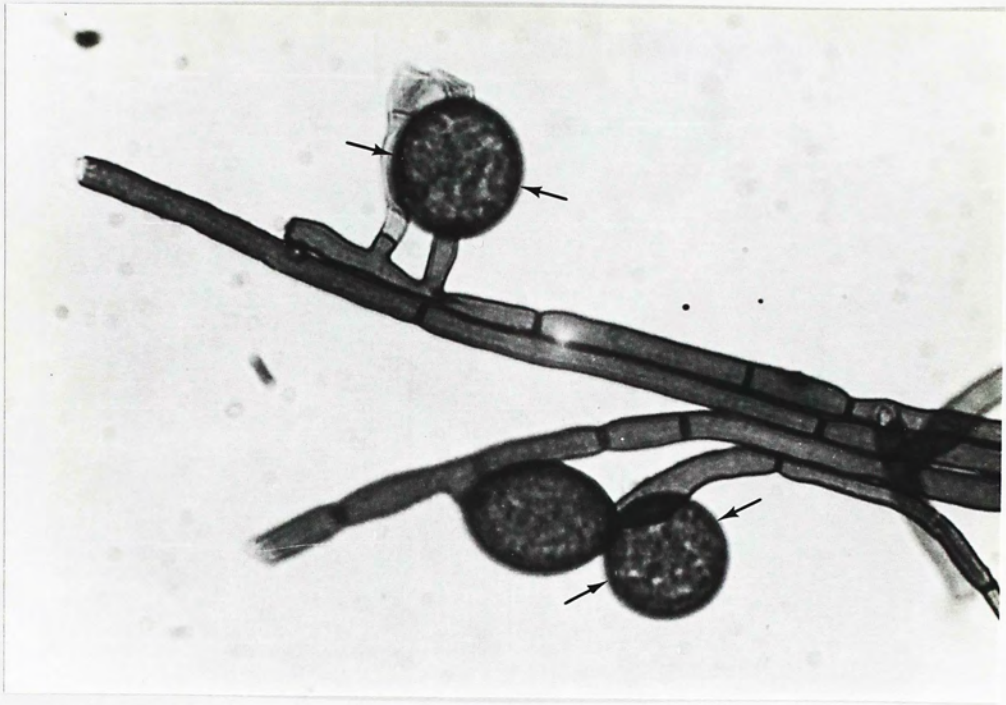


Figure 4.18 Parasympodiella laxa
(average diameter of conidia = 26.0 µ m).

Figure 4.19 *Penicillium wortmanii* on malt extract agar.

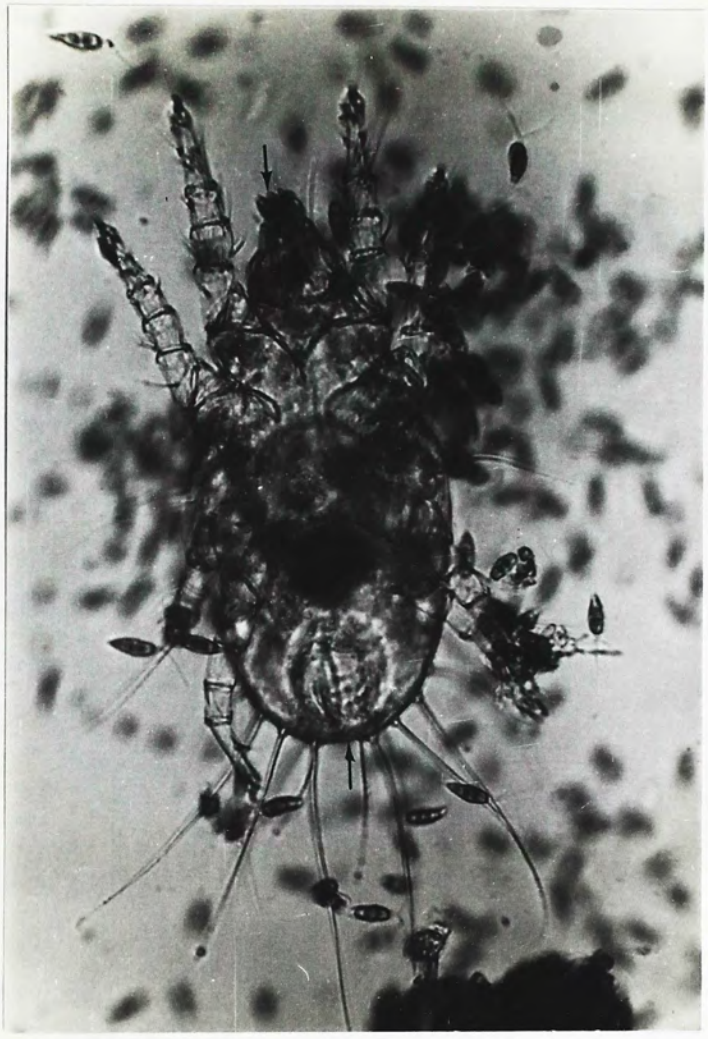


Figure 4.20 Tyrophagus sp. associated with fungal subcultures.
(length of body = 207.0 μm).

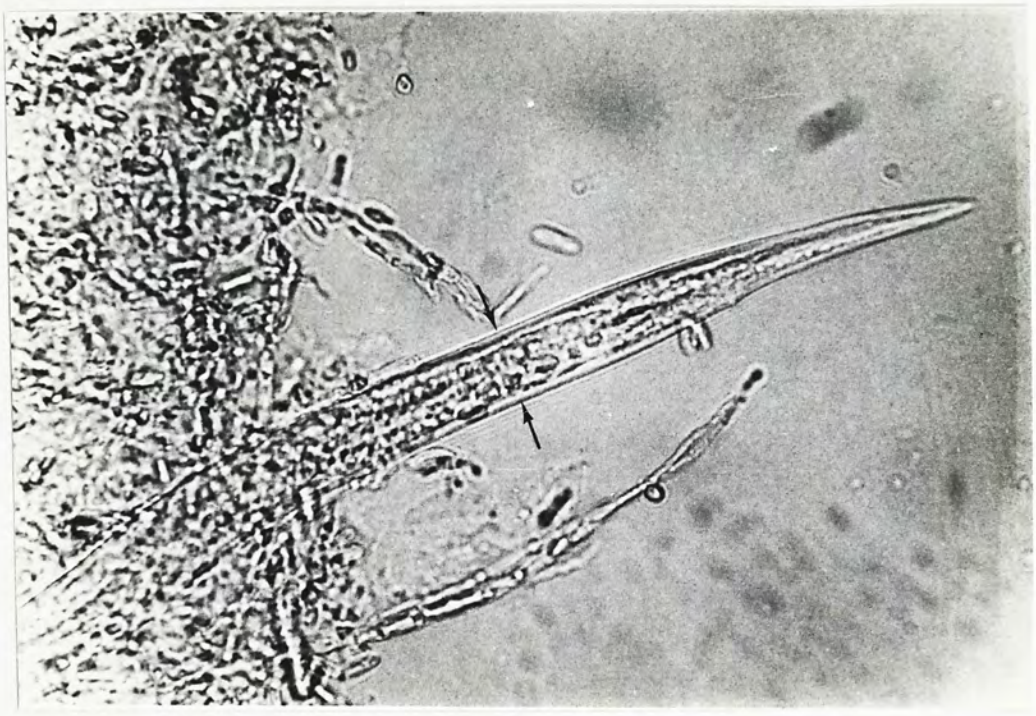


Figure 4.21 Nematode associated with fungal subcultures. (distance between arrows = 12.7 μm).

Figure 4.22 Interaction among surface and internal colonizers on *Rhodomyrtus* litter and fresh senescent leaves.

(B) Surface colonizers : *Trichoderma* spp. and *Mucor* spp.

(C) Internal colonizers : *Colletotrichum* spp. and *Phomopsis* spp.

Trichoderma spp. and *Colletotrichum* spp.

Mucor spp. and *Phomopsis* spp.

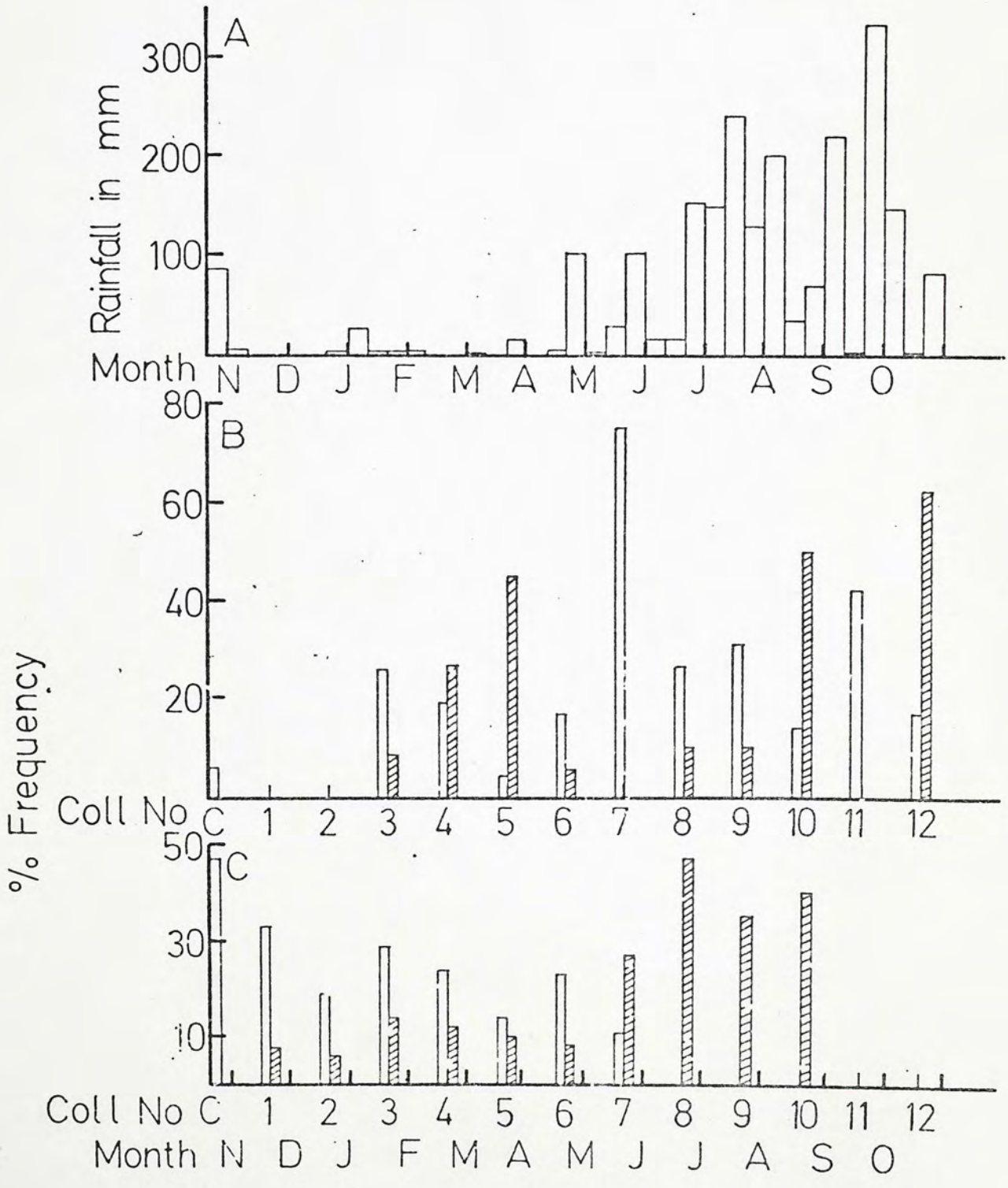

A
300
200
100
Rainfall in mm
Month N D J F M A M J J A S O
B
80
60
40
20
% Frequency
Coll No C 1 2 3 4 5 6 7 8 9 10 11 12
C
50
30
10
Coll No C 1 2 3 4 5 6 7 8 9 10 11 12
Month N D J F M A M J J A S O

Table 4.1 Percentage frequency of major species on control collections.

(The Figures represent percentage frequency of a species in each collection.)

0 = absent

1 = 1 - 10%

2 = 11 - 20%

and so on.

Month Coll. No.	Oct. Control	Nov. 1	Dec. 2	Jan. 3	Feb. 4	Mar. 5	Apr. 6	May 7	Jun. 8	Jul. 9	Aug. 10	Sep. 11	Oct. 12
A. Surface species													
1. *Pestalotia* spp.	2	4	0	2	0	2	3	3	2	2	1	2	2
2. *Phialophora fastigiata*	1	0	0	1	1	2	2	2	2	1	1	1	1
3. *Sterile sp. B*	3	1	0	2	0	0	1	0	1	1	1	2	1
4. *Trichoderma* spp.	1	2	0	0	1	0	1	0	2	1	1	1	1
5. *Aspergillus niger*	0	1	0	1	0	0	0	1	2	3	2	2	1
6. *Penicillium* sp.	1	1	0	2	0	0	0	1	0	0	1	1	0
7. *Fusarium sp. A.*	2	0	0	0	1	1	0	3	0	0	1	0	1
8. *Curvularia* spp.	1	0	0	0	2	0	1	1	0	0	1	1	1
9. *Fusarium oxysporum*	1	1	0	0	0	1	0	0	0	0	1	0	1
10. *Trichoderma viride*	1	0	0	0	2	0	0	0	3	0	1	0	1
11. *Nigrospora* sp.	1	0	0	0	2	1	1	0	0	0	1	0	0
B. Internal species													
1. *Colletotrichum sp. A.*	6	0	0	4	4	4	5	0	3	6	3	0	1
2. *Colletotrichum sp. B.*	0	0	0	0	0	0	0	0	0	2	5	7	10

Table 4.2 Percentage frequency of major species in litter samples set out in the dry season.

(The figures represent percentage frequency of a species in each collection.)

0 = absent

1 = 1 - 10%

2 = 11 - 20%

and so on.

Month Coll. No.	Oct. Control	Nov. 1	Dec. 2	Jan. 3	Feb. 4	Mar. 5	Apr. 6	May 7	Jun. 8	Jul. 9	Aug. 10	Sep. 11	Oct. 12
A. Surface species													
1. Sterile sp. B	3	1	2	0	0	0	0	0	0	0	0	0	0
2. Pestalotia spp.	2	4	3	3	0	0	2	0	1	0	0	0	0
3. Fusarium sp. A.	2	1	0	0	2	0	1	0	1	0	0	0	0
4. Penicillium thomii	1	0	3	2	1	0	1	0	0	0	0	0	0
5. Phialophora fastigiata	1	2	2	1	0	6	1	0	2	0	0	0	0
6. Penicillium sp.	1	1	1	0	0	0	2	0	1	0	0	2	0
7. Trichodema viride	1	0	0	2	2	0	0	3	1	0	0	0	0
8. Mucor hiemalis	0	0	0	0	3	5	0	0	0	0	3	1	1
9. Trichoderma glaucum	0	0	0	0	0	0	0	5	0	0	0	0	0
10. Trichoderma spp.	1	0	0	0	0	1	2	0	2	4	1	3	1
11. Mucor spp.	0	0	0	0	0	0	1	0	2	2	3	0	3
12. Trichoderma koningii	0	0	0	0	0	0	0	0	0	0	0	2	2
13. Mucor circinelloides	0	0	0	0	0	0	0	0	0	0	0	0	2
B. Internal species													
1. Colletotrichum sp. A.	5	4	2	3	3	2	3	2	0	0	0	0	0
2. Sterile sp. D.	1	5	2		2	1	1	0	0	1	0	0	0
3. Phomopsis sp. A	0	1	1	0	1	1	1	2	5	2	2	0	0
4. Phomopsis psidii	0	0	0	2	0	1	0	2	2	0	4	0	0

Table 4.3 Percentage frequency of major species in litter samples set out in the wet season.

(The figures represent percentage frequency of a species in each collection.)

0 = absent

1 = 1 - 10%

2 = 11 - 20%

and so on.

Month Coll. No.	Apr. Control	May 1W	Jun. 2W	Jul. 3W	Aug. 4W	Sep. 5W
A. Surface species						
1. *Pestalotia* spp.	2	1	0	0	0	0
2. *Fusarium oxysporum*	1	3	0	1	2	0
3. *Fusarium* sp. A.	1	2	0	2	5	0
4. *Mucor circinelloides*	0	0	0	2	1	0
5. *Mucor hiemalis*	2	0	0	2	0	0
6. *Trichoderma* spp.	0	0	0	0	5	4
B. Internal species						
1. *Collectotrichum* sp. A.	4	2	2	4	0	0
2. *Phomopsis* sp. A.	0	2	5	4	0	0
3. *Scolecobasidium humicola*	0	0	0	3	2	0
4. *Beltraniella nilgirica*	0	0	0	0	5	0
5. *Parasympodiella laxa*	0	0	0	0	0	6

Table 4.4 Percentage frequency of major species in surface soil from beneath litter samples in the dry and wet seasons.

(The figures represent percentage frequency of a species in each collection.)

0 = absent

1 = 1 - 10%

2 = 11 - 20%

and so on.

Month Coll. No.	Nov. 1	Dec. 2	Jan. 3	Feb. 4	Mar. 5	Apr. 6	May 7	Jun. 8	Jul. 9	Aug. 10	Sep. 11	Oct. 12
A. Dry Season												
1. *Penicillium thomii*	0	2	3	0	0	0	0	1	0	2	0	0
2. *Penicillium wortmanii*	0	1	1	1	5	0	2	1	0	1	4	0
3. *Penicillium* sp.	1	0	3	0	0	0	0	0	0	1	2	0
4. *Trichoderma viride*	8	7	1	0	0	0	1	6	0	0	0	0
5. *Trichoderma hamatum*	0	0	0	0	0	0	5	0	0	0	0	0
6. *Trichoderma koningii*	0	0	2	0	3	0	0	0	0	2	3	0
7. *Neurospora crassa*	0	0	0	0	0	0	2	0	0	1	0	0
8. *Phialomyces macrosporus*	0	0	1	0	0	0	0	0	0	2	0	0
B. Wet Season												
1. *Penicillium wortmanii*	0	0	0	0	0	0	2	2	0	0	4	0
2. *Trichoderma viride*	0	0	0	0	0	0	5	0	0	0	0	0
3. *Trichoderma hamatum*	0	0	0	0	0	0	2	0	0	0	1	0
4. *Trichoderma koningii*	0	0	0	0	0	0	1	1	0	0	2	0
5. *Trichoderma* spp.	0	0	0	0	0	0	0	3	0	0	2	0

CHAPTER 5

LITTER DECOMPOSITION: SUCCESSION OF THE FAUNA

The fauna involved in litter decomposition include a variety of forms such as the protozoans, nematodes, oligochaetes, micro- and macro- arthropods and terrestial molluscans. Each of these groups has its specific habitat and role in litter decomposition: for example, nematodes may be bacterivores or fungivores; oligochaetes are important in mixing organic and mineral soils in temperate regions. However, the most numerous groups are the microarthropods and macroarthropods. The term microarthropod is used to include mainly the collembolans and mites which are the most abundant animals obtained from the extraction of plant litter. It may also include animals in the classes Diplura, Thysanura and Protura, Symphyla and Pauropoda, and Tardigrada (Harding and Stuttard, 1974). The main groups of macroarthropods which play a dominant role include the larvae and adults of the Isopoda, Diplopoda, Isoptera, Diptera and Coleoptera. In addition, Thysanoptera, Hemiptera and Trichoptera may also play a part (Edwards, 1974). Consequently, emphasis was placed on the microarthropods and macroarthropods in the present study on the succession of the fauna.

Most of the quantitative studies of animals from plant litter were done by extraction with the Berlese- Tullgren funnel (Crossley and Hoglund, 1962; Gasdorf and Goodnight, 1963; McColl,1974 and Witkamp and Crossley,1966).However,owing to the diversity

of form and the mobility of animals, the quantity recovered by extraction may be an underestimate of the actual number which fed on the plant litter at one time or another. Consequently, the successional change of organisms during decomposition of litter is not so well established as in the case of the mycoflora. Nevertheless, extraction does reveal information on the groups of animal which feed frequently on the decomposing litter.

Materials and Methods

a) Dry season samples

The method of collecting litter and soil from the field has been dealt with in Chapter 3. After the samples had been taken back to the laboratory, the bag of leaves designated for colonization studies was emptied into a Tullgren funnel for extraction of animals. The equipment is shown in Figure 5.1: the funnel was 14 cm in diameter, and the container above the funnel was 13 cm in diameter and 16 cm in height. The partition between the container and the funnel was wire gauze with 3 mm mesh size, and the heat source was a 40 Watt incandescent lamp. In order to avoid killing the animals before they were able to escape, the light bulb was raised to a distance of 10 cm. Paper was used to seal the top of the container and thus prevent organisms in the laboratory from flying into the funnel. A covered vial containing 75% ethyl alcohol was

placed under the funnel to collect and preserve the animals falling through the funnel. The sample was left in the funnel for two weeks. Alcohol was added from time to time during the two weeks to replace that which had evaporated.

Animals collected in the vials were separated into groups. Animals which were left in the upper container because they were too big to pass through the 3 mm mesh were picked out. Insects were put into freshly prepared 75% ethyl alcohol, while mites were left in lactophenol to become transparent for examination. Then the specimens were identified. The references for identification were Balogh (1972), Barker and Wharton (1952), Beier (1932), Borror and White (1970), Chinery (1973), Chu (1949), CSIRO (1970), Ehara and Lee (1971), Emerton (1961), Evans (1961), Harris (1963), Kaston (1972), Lewis (1967), Pocock (1900), Savory (1964), Sherriffs (1934, 1935, 1936, 1938, 1939a and 1939b) and Stammer (1957 and 1963).

b) Wet season samples

The whole procedure of collection and extraction was repeated with the set of samples put out at the beginning of the wet season.

c) Soil samples

A sample of soil from beneath the mesh tray was also taken from the field at each collection. One portion was used for extraction of animals while the rest was plated out to isolate representatives of the soil mycoflora as

described in Chapter 4.

d) Control extractions

Two control extraction funnels were set up alongside the samples of litter and soil at Collection No. 12 in order to check the groups of animals present in the laboratory. In the first control, the light source was wrapped with paper as in the sample containers. In the second control, the container was fully exposed.

e) Animals captured in the field at each collection were also preserved and identified.

Results

The complete list of animals caught in the field at each collection, animals obtained from extraction of litter and soil from the dry season and the wet season is set out in Appendices 5.1, 5.2 and 5.3. The dry weight of litter of the dry-season set used for extraction decreased from 10.3 - 11.5 g in the earlier collections to 8.0 - 7.2 g in the later collections. The dry weight of litter of the wet-season set declined from 11.3 to 5.4 g. The amount of soil used varied from 250 to 275 g fresh weight. The figures reported were the actual number found in a particular collection.

a) Animals from the control funnels

Almost no animals were found in the vial placed under the control funnel which was sealed with paper as in the sample funnels. However, a large number of animals were

found in the second control which was fully exposed. The most numerous contaminating animals were leaf-hoppers belonging to the family Cicadellidae. The next most numerous were the flies belonging to the families Chironomidae, Ceratopongonidae, Cecidomyidae and Mycetophilidae. Beetles belonging to the families Tenebrionidae (Tribolium sp.) Pselaphidae and Scolytidae were also found, together with a chalcid wasp. Consequently, sealing the funnels may be assumed to exclude all or most extraneous animals so that animals appearing in the vials can be attributed to the samples of litter.

b) Animals captured in the field (Appendix 5.1)

Animals were frequently captured at the site where the mesh bags for studying decomposition were placed (decay site), and at Site 1 for litter collection during the monthly collections, although the number caught was not very great. Spiders were the most frequent, and they were caught regularly. The next most abundant animals were the isopods (family Porcellionidae) (Figure 5.2), which were caught mostly during the rainy season. Ants (family Formicidae) and cockroaches (Blattidae) were also frequent. Other captured animals included a few coleopterans, flies and other insects. A fairly large number of the mite Tyrophagus (Figure 5.3) was caught at the decay site in Collection No. 9, while a number of collembolans, Coleoptera larvae and Diptera larvae were caught at the decay site

during Collection No. 11. Most of these animals were the same as those obtained by extraction of plant litter.

c) Animals from extraction of litter in the dry season (Appendix 5.2)

The total number of animals in each collection was given in Table 5.1. It could be seen that there was an increase in the abundance of animals as decomposition progressed. The abundance at the advanced stages was due to larger number of some dominant species such as the Oribatulidae mite at Collection No. 10 and the Formicidae ant at Collection No. 11. In general mites and larval insects were more numerous in later stages which coincided with the wet season. The number of adult insects was smaller except at Collection No. 11, in which a large number of ants was recorded.

The more important groups of animals are given in Table 5.2

(i) Insecta. A diversity of insects was obtained from the litter. Important adult insects included cockroaches and flies. The family Chironomidae (Figure 5.4) was the most numerous representative of the Diptera. Larval Lepidoptera (Figure 5.5) was recorded throughout the latter half of the collections. The collembolans (families Entomobryidae and Sminthuridae) (Figures 5.6 and 5.7) were frequent and numerous. Larval Diptera (Figure 5.8)

together with the ants (family Formicidae) reached a peak at Collection No. 11. The isopods (family Porcellionidae) were important from Collection No. 8 onwards.

(ii) Acari. More mites were extracted during the latter half of the collections, which were made in the wet season. There were a number of important genera. The Mesostigmatic mite Typhlodromus (Figure 5.9) occurred regularly throughout with more in Collections No. 10 and 12. Another Mesostigmatic mite Ameroseius (Figure 5.10) was important throughout the latter half of the collections. The Astigmatic mite Tyrophagus was extracted during Collections No. 8, 9, 10 and 11, and was also found in association with fungal subcultures. By far the most abundant species was the Crytostigmatic mite belonging to the family Oribatulidae (Figure 5.11), of which 31 were isolated from Collection No. 10.

d) Animals from litter samples set out in the wet season (Appendix 5.2)

The total number of all animals is given in Table 5.3. Since only 5 collections were made, the number is smaller than that recorded for litter samples set out in the dry season. However, the average number of 39 animals per collection is similar to that of the dry season litter (Table 5.1).

The more important groups of animals are given in Table 5.4.

(i) Insecta. There were only a few important families of insects. Thysanoptera was recorded only once, at the first collection. The chironomid flies were important as in the other litter samples. The collembolans were important in all collections. Since the number of collections was small, no successional change was obvious.

(ii) Acari. As in the other samples, Tyrophagus was a very important genus of mites found both in the litter and the soil. Oribatulidae was also important as in the set of samples set out at the beginning of the dry season. There was one important species, Asca aphioides (Figure 5.12), which was also important in the other samples, but not so numerous as in this set. The Mesostigmatic mite Eutrachytes was recorded in the last two collections.

e) Animals from extraction of surface soil under litter samples set out in the dry season (Appendix 5.3)

The total number of all animals is given in Table 5.5. Comparing the relative abundance of the three major groups, mites were the most abundant. Immature insects were intermediate in number, while adult insects were the least numerous. The total number of mites was about twice that of the immature and adult insects added together.

(i) Insecta. In contrast insects were less numerous in the surface soil than in the litter. They were recorded only in small numbers, except the collembolans and the ants. Collembolans (especially the family Entomobryidae) were important throughout, but ants became important only at the beginning of the wet season.

(ii) Acari. Mites were more numerous in soil than in litter samples. They were represented by a number of important genera. Acugamassus (Mesostigmata) (Figure 5.13) was numerous in the earliest collections. Oribatulidae (Cryptostigmata) was numerous and important throughout. Belbidae (Cryptostigmata) (Figure 5.14) occurred in early collections, but reached a peak at the last collection. Tyrophagus, as in the litter samples and fungal subcultures, reached a maximum number of 22 in Collection No. 9. Immature Cryptostigmata was also important especially at the last collection.

f) Animals from surface soil under litter samples set out in the wet season (Appendix 5.3)

The total number of all animals is given in Table 5.7, and was similar to that of the surface soil under litter samples in the dry season.

The more important groups of animals are named in Table 5.8.

(i) Insecta. As in the other set of soil samples, collembolans and ants were most important. In addition, chalcid wasps were also of some importance.

(ii) Acari. Important mites were represented by a number of genera and families. Tyrophagus again was numerous, and reached a maximum number at Collection No. 3W, at the same time in surface soil under Collection No. 9. The families Belbidae and Oribatulidae were represented by many individuals.

Discussion

Before considering the fauna in detail, the validity of the results obtained by extracting the animals by means of the Tullgren funnel should be examined. In a review of the role of macroarthropods in decomposition of litter in temperate regions under deciduous woodlands, Edwards (1974) reported that coleopteran adults and larvae, and dipteran larvae, were the most important insects, but adult dipterans were not recorded. However, in the present study, a number of adult flies, especially of the family Chironomidae, was obtained from extraction. Nevertheless, there is adequate evidence to show that the adult flies were present in the litter. First, although numerous dipterans and other animals were obtained in the vial placed under the control funnel which was fully exposed (and thus may collect a variety of insects found in the laboratory), no animals were obtained in the

vial placed under the control funnel which was sealed as were the sample funnels, indicating that the sample funnels were well protected from intruding insects. Secondly, large flies in the family Calliphoridae and large beetles of the families Reduviidae and Scarabaeidae (with a length up to 8 mm) had been caught while emptying the litter samples into the extraction apparatus. Some of the large insects had also been caught in the field. Lastly, the litter samples and surface soil were put side by side for extraction, but far fewer insects were obtained from the soil samples than from the litter samples. We can conclude, therefore, that some species of insects were common to both field and laboratory.

Although there was no clear-cut change from one major group of animals to another in litter samples set out in the dry season, a successional change in the diversity of animals was observed. Very few groups of animals colonized the litter during the first half of the experiment, which coincided with the dry season. However, during the latter half of the experimental period, both the diversity and number of each group, was increased. The number of taxa increased from a total of 24 to a total of 45 as the litter decayed. The macroarthropods, Blattidae and Mycetophilidae gave way to the Isopoda, the Chironomidae, the Formicidae, larval forms and the collembolans Entomobryidae and Sminthuridae. Crossley and Hoglund (1962), and Crossley and Witkamp (1964) also reported that few species of microarthropods colonized litter during the early stages

but the diversity increased later as litter progressively decayed.

Anderson (1975) has studied the succession and diversity of fauna on Fagus and Castanea leaves, but he was unable to establish a successional change from one major group of animals to another, but successional change was obvious in some species of Cryptostigmatic mites; for example, Platynothrus, Steganacarus, Phthiracarus and Eniochthonius showed an increase while Carabodes, Chamobates, Tectocepheus and Adoristes showed a progressive decrease. Successional change in the present study was obvious in only two families of Mesostigmatic mites. Typhlodromus sp. of the family Phytoseiidae increased in the litter as time passed; Acugamassus sp. of the family Rhodacaridae, which is considered as a predacious family, showed a decrease in soil during the wet season.

When the fauna of the litter and soil was compared, we can see that the increase in the number of taxa in surface soil was not so marked as in litter; in fact a number of them occurred throughout both dry and wet seasons with the exception of the Formicidae and Tyrophagus which were only active in the wet season. This difference in the litter and soil fauna brings up the point that soil is a relative stable entity in terms of nutrient substrates, while litter at different stages of decomposition is much more heterogeneous. The heterogenicity of nutrient substrates also supports a greater number and variety of the feeding fauna. McColl (1974) studied the arthropods in six forest types on the West Coast of New Zealand

and reported that, under a podocarp/beech forest, the largest number of arthropod groups were found in the partly decomposed litter.

In addition to being nutritionally essential, litter is also important in providing a greater variety of habitats for the fauna. Gasdorf and Goodnight (1963) studied the abundance and diversity of arachnids in an oak-hickory climax forest (with a dominant vegetation of Quercus alba, Q. borealis, Q. velutina and Carya cordiformes), and that in a flood plain (with a dominant vegetation of Ulmus americana, Acer saccharum, Platanus occidentalis and Salix sp.) where the litter layer was swept away annually by floods. They reported that the climax forest supported a greater number and a greater variety of species of arachnids than the vegetation of the flood plain. They therefore concluded that the litter layer was important for protection from predation and desiccation, and for egg-laying as well as for food. This result points up the fact that not all animals found in litter are feeding upon it. Results from the present study are summarized in Table 5.9 and suggest that some of the earlier colonizers, such as the Blattidae, may be only 'wanderers', while many of the later colonizers on the more decomposed litter come from the soil —— especially mites in the families Oribatulidae and Ascaridae (Tyrophagus). Nevertheless, there is a close relationship between the occurrence and feeding habit of the fauna. Larval insects, cockroaches, chironomid flies and the isopods were found to be more

numerous in the litter layer in the present study. Larvae, especially those of the flies, feed mainly on fresh and decomposing leaves. Some other dipteran larvae, especially of the Mycetophilidae, feed on fungi associated with decaying wood. Similarly, Coleoptera may also be important in the breakdown of decaying wood. Isopods are omnivorous crustaceans feeding on decaying and faecal materials. They are confined to sheltered and moist habitats. Therefore, they are less active in the dry season. Blattidae are also omnivorous, though they are mainly detritus-feeders, consuming plant remains above ground. Similarly, the microarthropods also have their preference. Some feed on fungi (for example, Belbids on Trichoderma konigii); some feed on less decomposed litter while others feed on more decomposed material. However, it seemed that the majority preferred to feed on moist, partially decomposed litter.

Thus, as litter accumulates under a vegetation formation, the variety of food and habitats will become greater. This will then support a greater variety of species. Species inhabiting the litter will show sequential change as freshly fallen litter decays progressively or seasonally as in the present study.

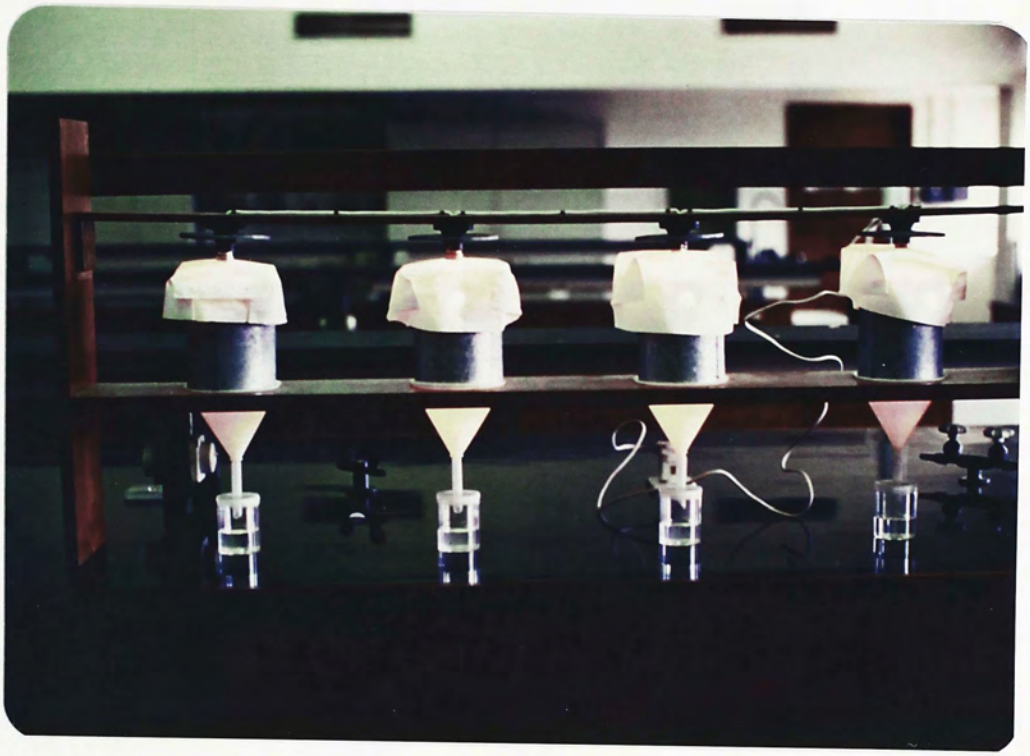


Figure 5.1 The Tullgren funnel for extraction of animals from plant litter and surface soil.

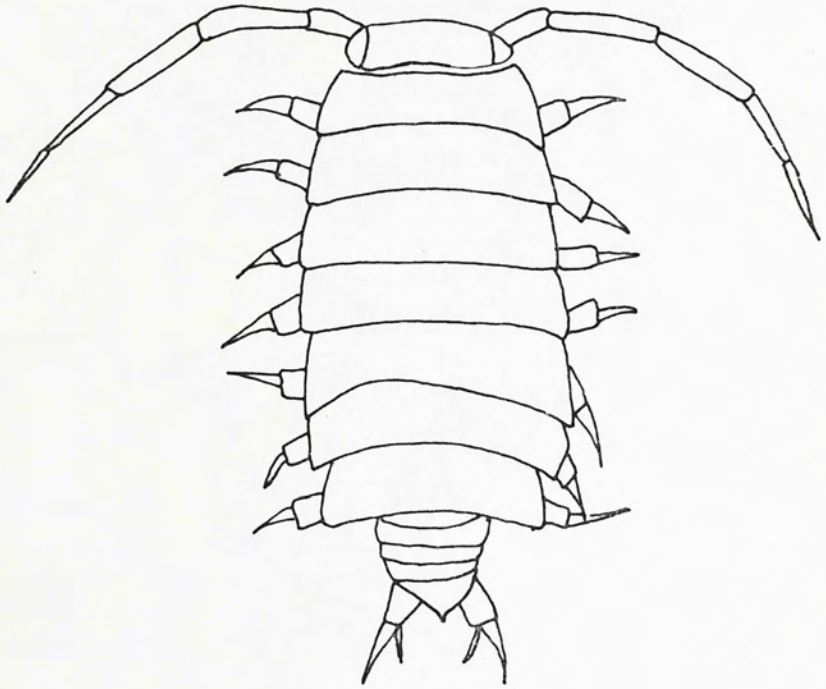


Figure 5.2 The woodlouse

Class Malacostraca
Order Isopoda
Family Porcellionidae

(length of body = 8.35 mm).

Figure 5.3 Tyrophagus sp.

Class Arachnida
Subclass Acari
Order Astigmata
Family Acaridae

(length of body = 0.37 mm).

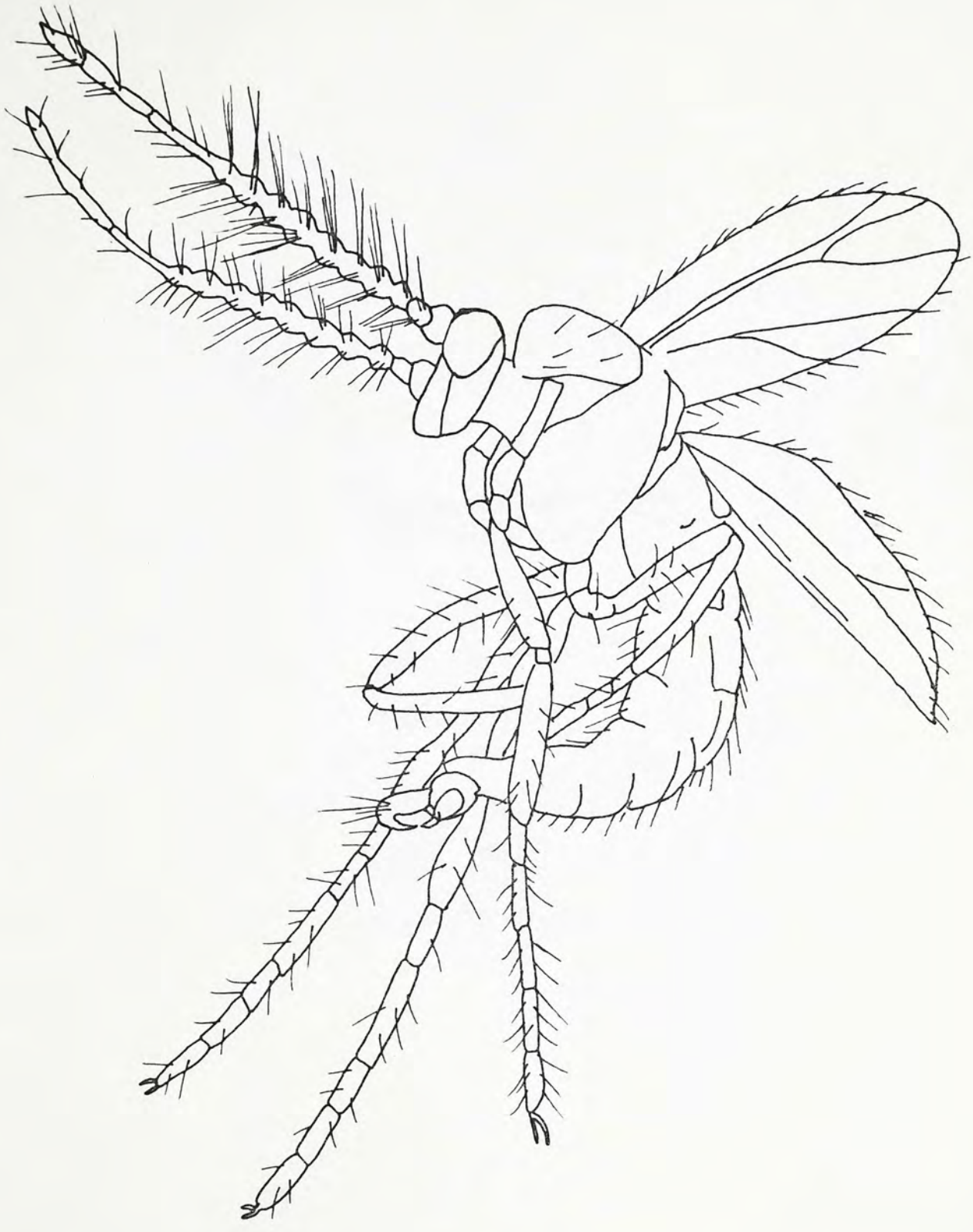


Figure 5.4 Chironomid fly

Class Insecta
Order Diptera
Family Chironomidae

(length of body = 1.35 mm).

Figure 5.5 Larval Lepidoptera

Class Insecta
Order Lepidoptera

(length of body = 9.65 mm).

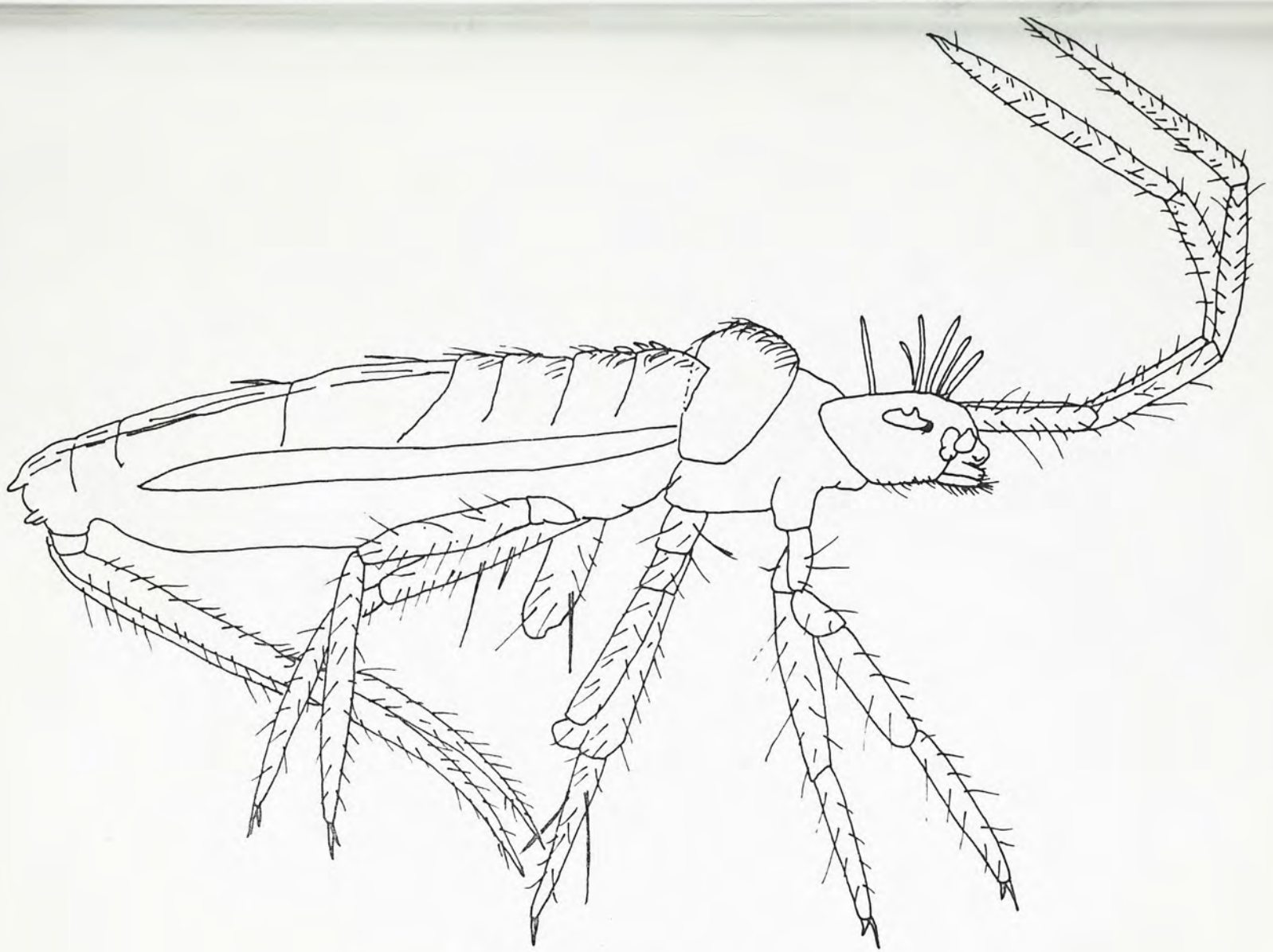


Figure 5.6 Collembolan

Class Insecta
Subclass Apterygota
Order Collembola
Family Entomobryidae
(length of body = 1.33 mm).

Figure 5.7 Collembolan

Class	Insecta
Subclass	Apterygota
Order	Collembola
Family	Sminthuridae

(length of body = 0.66 mm).

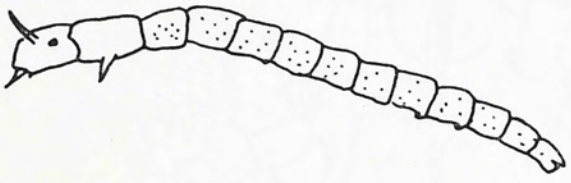


Figure 5.8 Larval Diptera

Class Insecta
Order Diptera

(length of body = 2.85 mm).

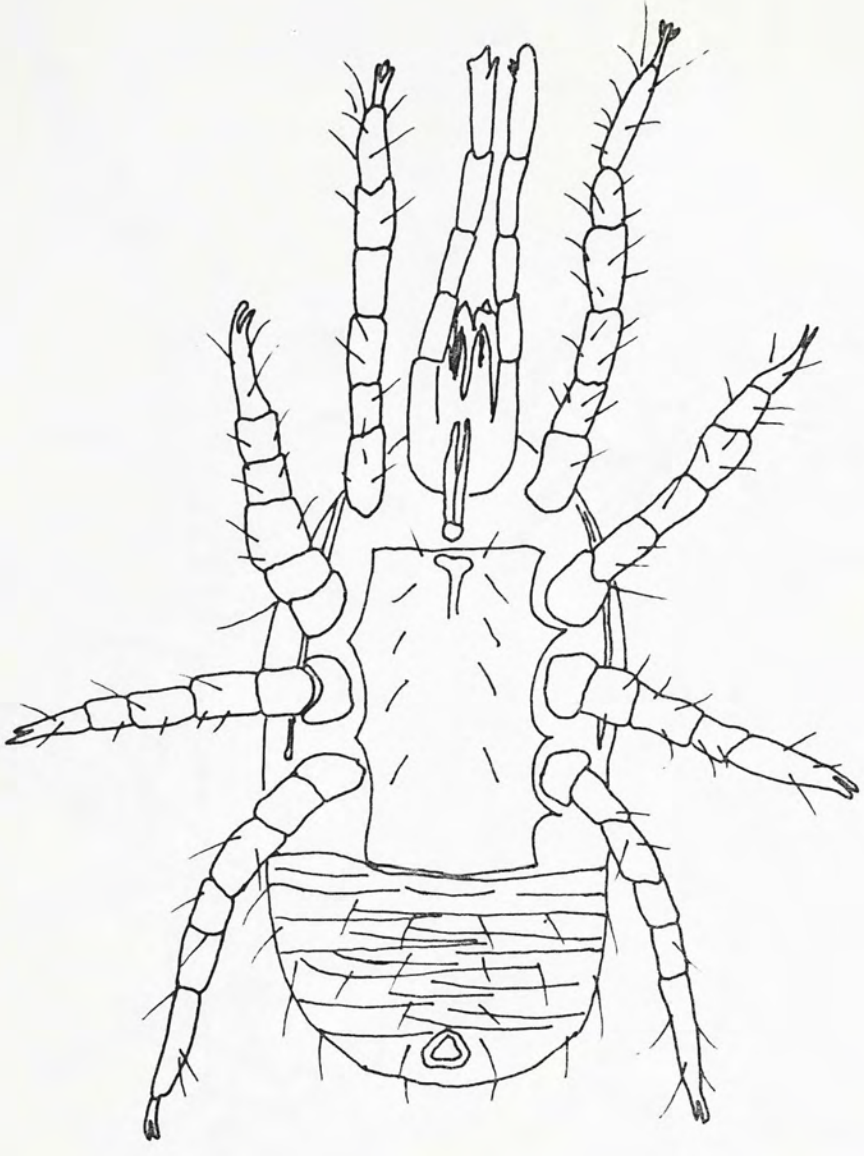


Figure 5.9 Typhlodromus sp.

Class	Arachnida
Subclass	Acari
Order	Mesostigmata
Family	Phytoseiidae

(length of body = 0.43 mm).

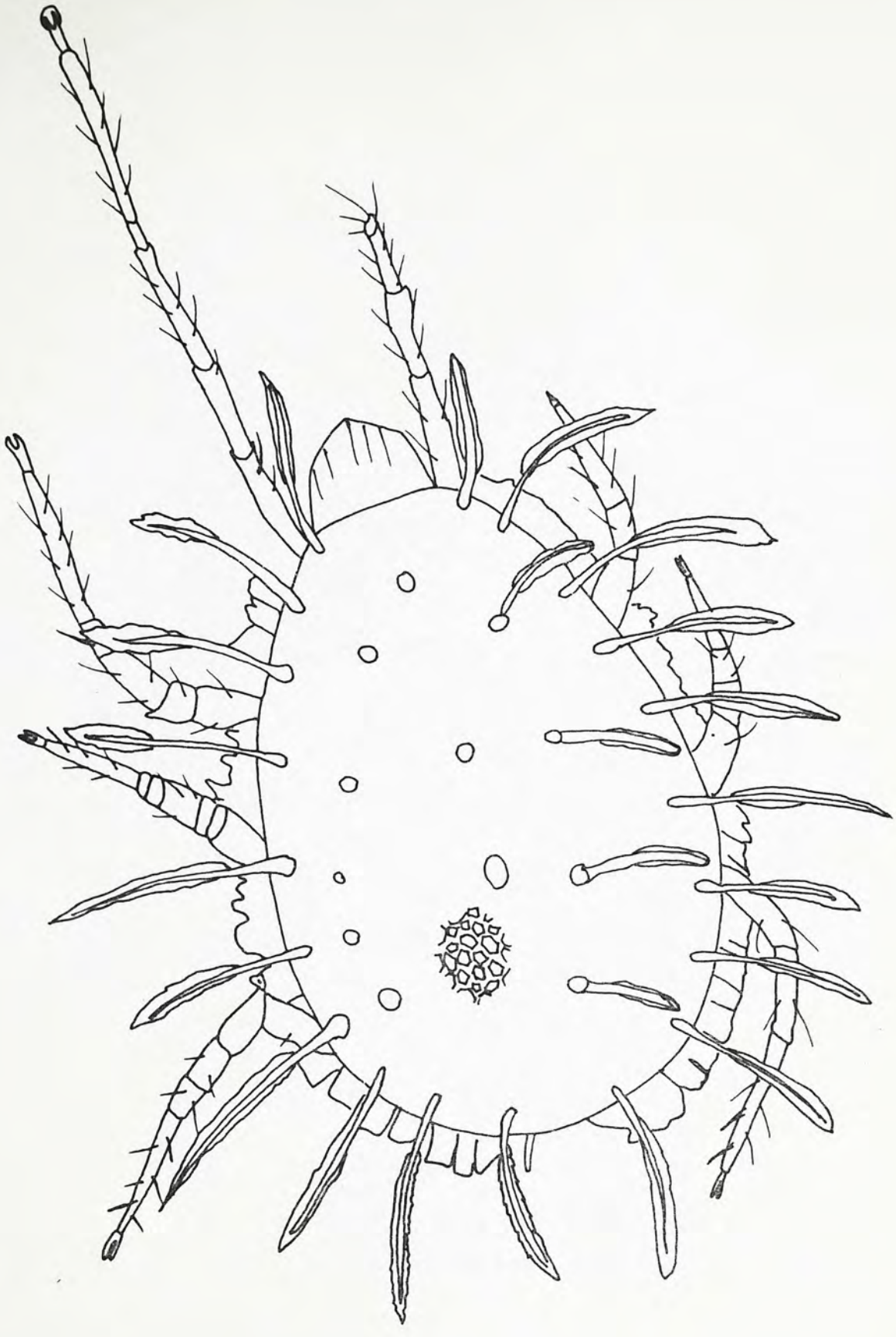


Figure 5.10 Ameroseius sp.

Class Arachnida
Subclass Acari
Order Mesostigmata
Family Ameroseiidae

(length of body = 0.46 mm).

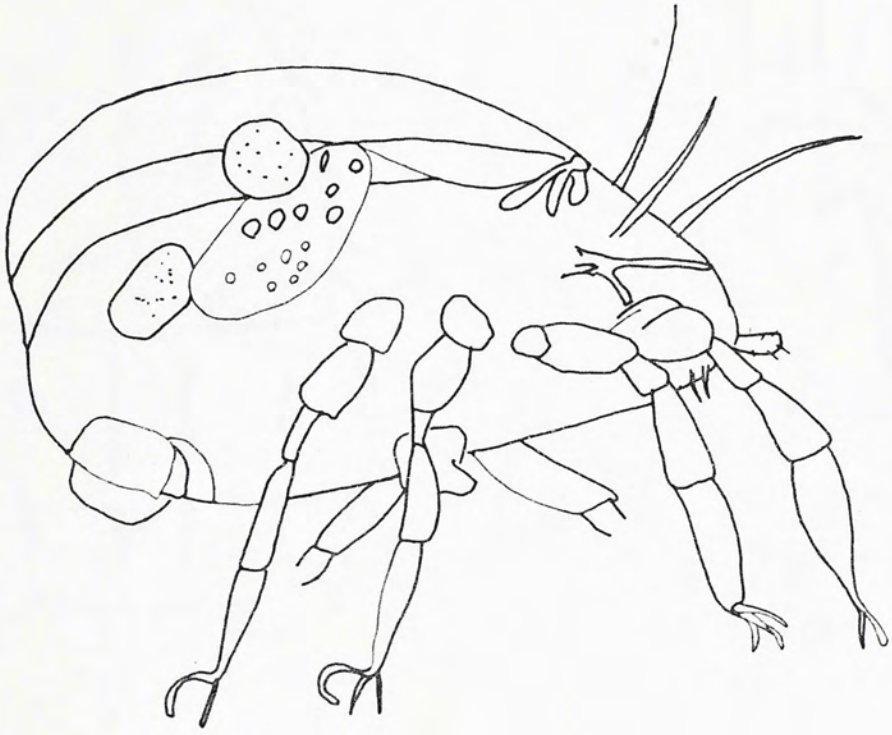
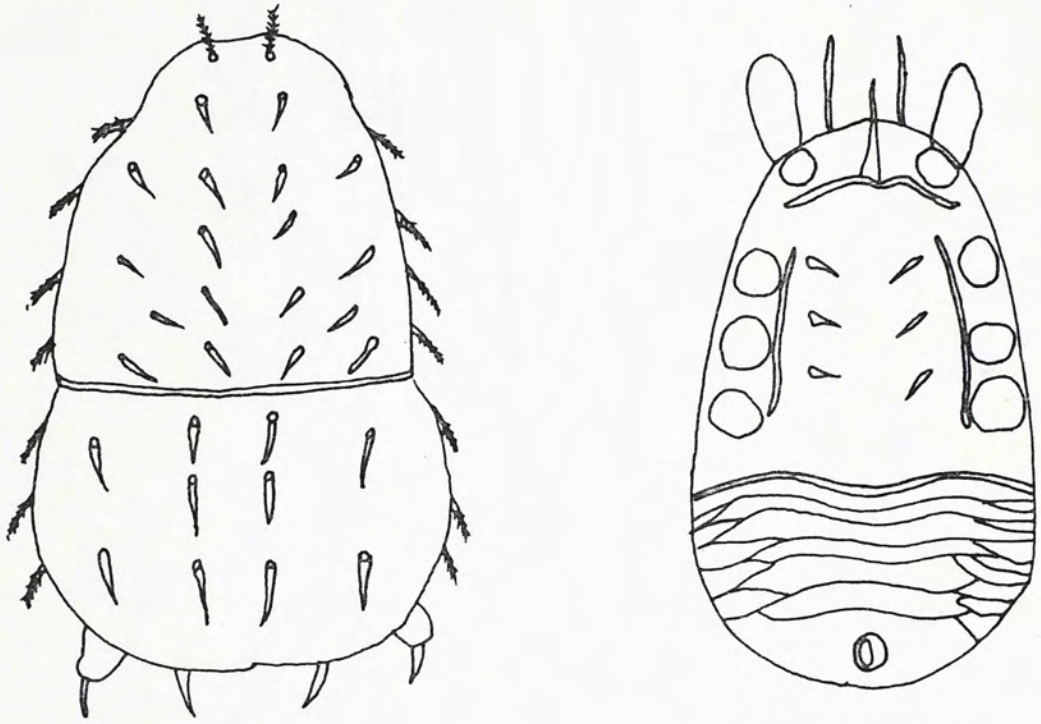


Figure 5.11 Oribatid mite

Class	Arachnida
Subclass	Acari
Order	Cryptostigmata
Family	Oribatulidae

(length of body = 0.43 mm).



a) Dorsal view b) Ventral view

Figure 5.12 Asca aphidioides

Class	Arachnida
Subclass	Acari
Order	Mesostigmata
Family	Ascaidae

(length of body = 0.34 mm).

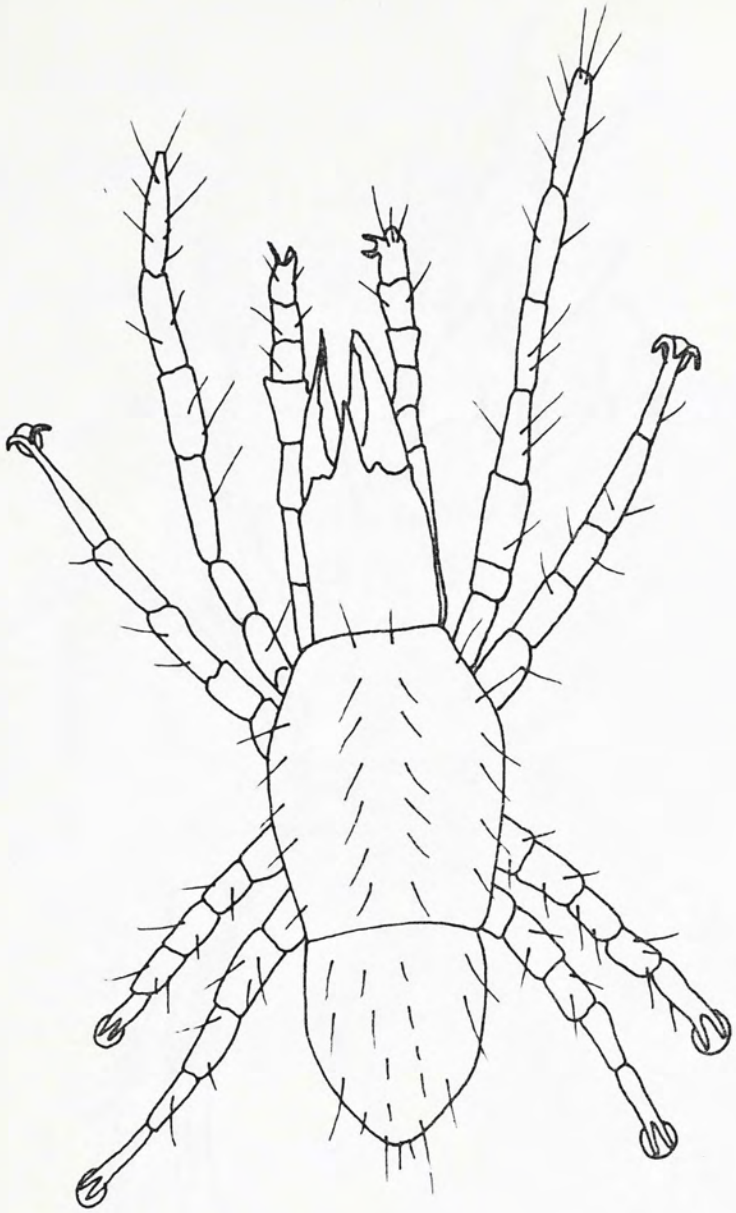


Figure 5.13 Acugamassus

Class	Arachnida
Subclass	Acari
Order	Mesostigmata
Family	Rhodacaridae

(length of body = 0.44 mm).

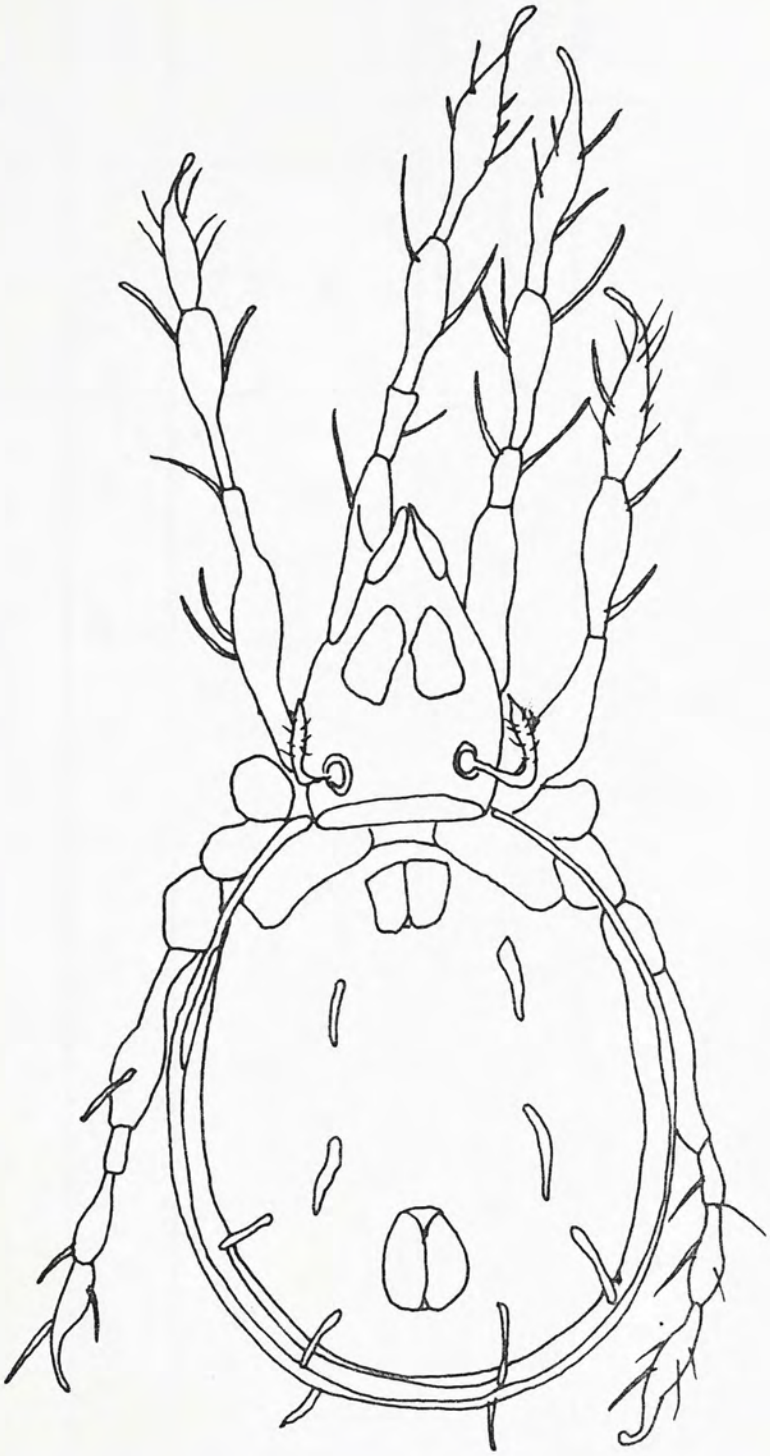


Figure 5.14 Oribatid mite

Class	Arachnida
Subclass	Acari
Order	Cryptostigmata
Family	Belbidae

(length of body = 0.24 mm).

Table 5.1 The total number of all animals from litter samples set out in the dry season.

Month / Coll. No.	Nov 1	Dec 2	Jan 3	Feb 4	Mar 5	Apr 6	May 7	Jun 8	Jul 9	Aug 10	Sep 11	Oct 12	Total of all collections
A. Class Insecta													
1. Immature insects													
a. Collembola						1	1	23	4	2	7	11	49
b. Other orders						2	1	6	4	6	27	4	50
c. Total immature insects						3	2	29	8	8	34	15	99
2. Adult insects													
a. Coleoptera					1	1	1				4	1	8
b. Diptera			1	2	10	5	10	1		8	19	7	63
c. Hemiptera			2		1	1	2	3				4	13
d. Hymenoptera					2	2	3				30		37
e. Other orders			2	1	4	3		1		3		1	15
f. Total adult insects			5	3	18	12	16	5		11	53	13	136
3. Total insects			5	3	18	15	18	34	8	19	87	28	235
B. Class Arachnida													
1. Subclass Acari													
a. Astigmata							1		3	5	3		12
b. Prostigmata					1					1	3		5
c. Mesostigmata		2	1		1	4		7	14	30	9	16	84
d. Cryptostigmata		1				1		31	7	38	6	15	99
e. Total Acari		3	1		2	5	1	38	24	74	21	31	200
2. Other arachnids					1	1		1	1		2	1	7
3. Total arachnids		3	1		3	6	1	39	25	74	23	32	207
C. Other classes						2	1	14	4	1	4	5	31
D. Total of all animals in each collection		3	6	3	21	23	20	87	37	94	114	65	473

Table 5.2 The more important families of animals from litter samples set out in the dry season.

Month / Coll. No.	Nov 1	Dec 2	Jan 3	Feb 4	Mar 5	Apr 6	May 7	Jun 8	Jul 9	Aug 10	Sep 11	Oct 12
A. Class Insecta												
1. Blataria												
Blattidae			2	1	4	3				3		
2. Diptera												
Mycetophilidae			1	1	2	1					3	2
Psychodidae				1	1		2	1			1	4
Chironomidae					3	1				8	12	
3. Larval Lepidoptera							1	2	1	1	1	1
4. Larval Coleoptera						2					6	2
5. Collembola												
Entomobryidae							1	1	4		5	
6. Larval Diptera								3		3	14	
7. Collembola												
Sminthuridae								21		2	1	11
8. Hymenoptera												
Formicidae											26	
B. Class Arachnida												
1. Phytoseiidae												
Typhlodromus sp.		2	1			2			1	13		8
2. Ameroseiidae												
Ameroseius sp.						2		6	11	10		1
3. Acaridae												
Tyrophagus sp.							1		3	5	3	
4. Oribatulidae								28	7	31	1	10
C. Class Malacostraca												
Isopoda												
Porcellionidae								11	4	1	4	5

Table 5.3 The total number of animals from litter samples set out in the wet season.

Month / Coll. No.	May 1w	Jun 2w	Jul 3w	Aug 4w	Sep 5w	Total of all collections
A. Class Insecta						
1. Immature insects						
a. Collembola		5	4		10	19
b. Other orders		6		1	2	9
c. Total immature insects		11	4	1	12	28
2. Adult insects						
a. Coleoptera		1			2	3
b. Diptera	4	10	7		4	25
c. Hemiptera	2	1			1	4
d. Hymenoptera	1	2	1		2	6
e. Other orders	6					6
F. Total adult insects	13	14	8		9	44
3. Total insects	13	25	12	1	21	72
B. Class Arachnida						
1. Subclass Acari						
a. Astigmata		9	14	4	4	31
b. Prostigmata			1			1
c. Mesostigmata		20	4	5	14	43
d. Cryptostigmata		7	7	5	21	40
e. Total Acari		36	26	14	39	115
2. Other arachnids				3		3
3. Total arachnids		36	26	17	39	118
C. Other classes	2	1			2	5
D. Total of all animals in each collection	15	62	38	18	62	195

Table 5.4 The more important families of animals from litter samples set out in the wet season.

Month Coll. No.	May 1w	Jun 2w	Jul 3w	Aug 4w	Sep 5w
A. Class Insecta					
1. Thysanoptera	4				
2. Diptera					
Chironomidae		1	7		2
3. Collembola					
Entomobryidae		5	3		1
4. Collembola					
Sminthuridae			1		8
B. Class Arachnida					
1. Acaridae					
Tyrophagus sp.		9	14	4	4
2. Oribatulidae		6	5	4	8
3. Ascaidae					
Asca aphidioides		19		1	8
4. Eutrachytidae					
Eutrachytes sp.				4	4

Table 5.5 The total number of animals from surface soil under litter samples set out in the dry season.

Month / Coll. No.	Nov 1	Dec 2	Jan 3	Feb 4	Mar 5	Apr 6	May 7	Jun 8	Jul 9	Aug 10	Sep 11	Oct 12	Total of all collections
A. Class Insecta													
1. Immature insects													
a. Collembola	16	12	11		2				5	2	17	3	68
b. Other orders	2	2	11		6	1			3		5	3	33
c. Total immature insects	18	14	22		8	1			8	2	22	6	101
2. Adult insects													
a. Coleoptera					1		2	1			1	1	6
b. Diptera		1	1	4	2	2	5					1	16
c. Hemiptera				1		2		1				1	5
d. Hymenoptera		1	1		3	10	3	1	6	22	2	1	50
e. Other orders	1			1		1	1						4
f. Total adult insects	1	2	2	6	6	15	11	3	6	22	3	4	81
3. Total insects	19	16	24	6	14	16	11	3	14	24	25	10	182
B. Class Arachnida													
1. Subclass Acari													
a. Astigmata									22		1	1	24
b. Prostigmata	6	2	2			1	1		2		2	14	30
c. Mesostigmata	25	14	20		3	2			4		5	7	80
d. Cryptostigmata	6	4	16		7	5			9		1	70	118
e. Total Acari	37	20	38		10	8	1		37		9	92	252
2. Other arachnids	1		2						1		4	2	10
3. Total arachnids	38	20	40		10	8	1		38		13	94	262
C. Other classes	3					7			2				12
D. Total of all animals in each collection	60	36	64	6	24	31	12	3	54	24	38	104	456

Table 5.6 The more important families of animals from surface soil under litter samples set out in the dry season.

Month	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
Coll. No.	1	2	3	4	5	6	7	8	9	10	11	12
A. Class Insecta												
1. Collembola												
Entomobryidae	2	8	3		2				4	1	14	2
Other families	14	4	8						1	1	3	1
2. Hymenoptera												
Formicidae					2	9	1	1	6	22	2	
B. Class Arachnida												
1. Rhodacaridae												
Acugamassus sp.	17	8	12		3	1					1	
2. Oribatulidae	4	2	14		2				8		1	2
3. Belbidae												
Plesiodameus sp.	2	1	1								11	
4. Galumnidae												
Allogalumna sp.		1	1		1	2					1	
5. Belbidae												
Bel 1 & 2					3	3					22	
6. Acaridae												
Tyrophagus sp.									22		1	1
7. Immature C1											8	
8. Immature C2											19	

Table 5.7 The total number of animals from surface soil under litter samples set out in the wet season.

Month Coll. No.	May 1w	Jun 2w	Jul 3w	Aug 4w	Sep 5w	Total of all collections
A. Class Insecta						
1. Immature insects						
a. Collembola	1	14	7	14	33	69
b. Other orders				2	2	4
c. Total immature insects	1	14	7	16	35	73
2. Adult insects						
a. Coleoptera	1	1			1	3
b. Diptera	6	2	1	2	13	24
c. Hemiptera	1	3				4
d. Hymenoptera	4	5	5	9	10	33
e. Other orders	3					3
f. Total adult insects	15	11	6	11	24	67
3. Total insects	16	25	13	27	59	140
B. Class Arachnida						
1. Subclass Acari						
a. Astigmata	1	5	24	1	2	33
b. Prostigmata	2	2	5	2	3	14
c. Mesostigmata	1	14	9	13	20	57
d. Cryptostigmata	1	40	15	56	23	135
e. Total Acari	5	61	53	72	48	239
2. Other arachnids	1	1	1	6	2	11
3. Total arachnids	6	62	54	78	50	250
C. Other classes	2	1		1	2	6
D. Total of all animals in each collection	24	88	67	106	111	396

Table 5.8 The more important families of animals from surface soil under litter samples set out in the wet season.

Month Coll. No.	May 1w	Jun 2w	Jul 3w	Aug 4w	Sep 5w
A. Class Insecta					
1. Hymenoptera Mymaridae	4	1	1		2
2. Hymenoptera Formicidae		4	3	9	8
3. Collembola Entomobryidae	1	12	3	7	24
4. Collembola Other families		2	4	6	9
B. Class Arachnida					
1. Acaridae *Tyrophagus* sp.	1	5	24	1	2
2. Belbidae *Plesiodameus* sp.	1	3	3	10	2
3. Belbidae Bel 1 & 2		9	1	7	
4. Oribatulidae		10	3	23	4
5. Phthiracaridae *Paratritia* sp.		13	1	3	
6. Galumnidae		2	6	6	
7. M1		4		4	2
8. Ascaidae *Asca aphidioides*			1	5	2
9. Rhodacaridae				1	11

Table 5.9 Comparison of the abundance of fauna in litter and soil.

1. LITTER FAUNA

Colonizers of early litter	Colonizers of more decayed litter
	Isopoda
Insecta	
Blattidae	
Mycetophilidae	Chironomidae
	Larval Coleoptera
	Larval Diptera
	Larval Lepidoptera
	Formicidae
	Entomobryidae
	Sminthuridae
Acari	
Typhlodromus sp.	Typhlodromus sp.
	Oribatulidae
	Ameroseius sp.
	Tyrophagus sp.
	Asca aphioides

2. SURFACE SOIL FAUNA

Colonizers in dry season	Colonizers in wet season
Insecta	
Entomobryidae	Entomobryidae
Other collembolans	Other collembolans
	Formicidae
Acari	
Acugamassus sp.	
Oribatulidae	Oribatulidae
Belbidae	Belbidae
	Tyrophagus
	Immature Ctyptostigmata

CHAPTER 6

GENERAL DISCUSSION

This chapter begins with a brief review of the relevant literature concerning the production and decomposition of plant litter. In the second section an attempt will be made to integrate the results from the present study and, where appropriate, to view it in relation to the results of others.

1. Review of the literature

a) Litter production

The earliest studies of litter production were on forest ecosystems, and these studies were usually made in conjunction with an investigation of other aspects of litter such as its chemical composition, its decomposition, or its relation to the productivity of the ecosystem. Ebermayer's work (1876) on the production and the chemical composition of litter, and Müller's work (1887) on the importance of litter production in relation to soil development were the earliest studies of the subject. Many other investigations have been made subsequently on litter production in forests and other ecosystems, and these studies have been documented in detail. For example, Lutz and Chandler (1946) have reviewed the importance of litter fall in ecosystems, while Bray and Gorham (1964) have

compiled a comprehensive review on litter production in the forests of the world.

Litter production in scrublands has been discussed in Chapter 2 in relation to litter production in the present study. The main results of the literature may be summarized as follows:

Scrubland community	Litter fall ($kg\ ha^{-1} yr^{-1}$)	Literature
Calluna heath (mature stage) (Dorset, southern England)	3180 (direct method)	Chapman (1967)
	2500 (indirect method)	Chapman et al (1975b)
Calluna heath (i) Forvie (ii) Kerloch Scotland	4330 1620 (air-dried wt.)	Cormack & Gimingham (1964)
Ulex europaeus community (New Zealand)	8880	Egunjobi (1971)
Adenostoma fasciculatum chaparral (western California)	2800	Kittredge (1955)
Quercus coccifera garrigue (southern France)	2300	Lossaint (1973)

There is a wide variation in the range of values obtained. Except for the very high value in *Ulex* litter and the very low value in *Calluna* heath at Kerloch, the amount of litter produced annually falls within the range 2000 - 4500 $kg\ ha^{-1}$.

b) Litter decomposition: physical and chemical aspects

The main object of studies on decomposition is to estimate the rate of release and recycling of nutrients. Initiation of decomposition studies may be attributed to Müller (1887) who investigated the influence of vegetation on soil development. Subsequent studies have been made on both lower and higher plant materials. However, the most extensive work has been done on angiospermous litter. Among the studies are those of Melin (1930), Chandler (1941, 1944), Jenny, Gessel and Bingham (1949), Kendrick (1959), Witkamp and van der Drift (1961), Nykvist (1963), Hayes (1965a), Bazilevich and Rodin (1966), Attiwill (1967), Will (1967), Cole, Gessel and Dice (1968), Duvigneaud and Denaeyer-De Smet (1970), Anderson (1973b), Ewel (1976) and Edwards (1977). An immense project was initiated in the 1960s to study the overall nutrient recycling in forested watersheds in the Hubbard Brook Forest, and from this over 200 papers have emerged already. The biogeochemical cycles for that forested ecosystem have been constructed and summarized by Likens, Bormann, Pierce, Eaton and Johnson (1977).

The rate of decomposition and mineral cycling depends on the species of plants under study and locality where they are found. Relevant information from a garrigue and from a deciduous forest in the Cool Temperate region is given below.

A. Garrigue in southern France (Lossaint, 1973)

I. Biomass = 23500 kg ha^{-1}

Litter fall = 2300 kg $ha^{-1}yr^{-1}$

(Litter fall/biomass) x 100% = 10 %

II. Mineral cycling

Cation content in kg ha^{-1}	Na	K	Mg	Ca
i) Ion in biomass	1.5	32.5	5.8	45.8
ii) Ion in litter fall per year	0.6	9.7	2.7	36.5
iii) $\frac{\text{Ion in litter}}{\text{Ion in biomass}}$ x 100%	40	30	46.5	79.7

B. Hubbard Brook Forest (Gosz et al,1973 ; Likens et al, 1977)

I. Rate of loss in dry weight per year for

i) Betula allegheniensis = 57.0%

ii) Acer saccharum = 40.0%

iii) Fagus grandifolia = 32.0%

II. Mineral cycling

Cation content in kg ha^{-1}	Na	K	Mg	Ca
i) Ion in biomass	1.6	155	36	383
ii) Ion in litter fall per year	0.1	18.3	5.9	40.7
iii) $\frac{\text{Ion in litter}}{\text{Ion in biomass}}$ x 100%	6.2	11.8	16.4	10.6
iv) Rate of release of cations by decomposition per year	-	2.78	0.97	0.91
v) Percentage of ion in biomass released per year	-	1.79	2.69	0.02

The garrigue cited is situated in southern France around the shore of the Mediterranean Sea. It has a humid and cool winter, and a hot summer that is usually dry. The dominant shrub is the evergreen Quercus coccifera. The Hubbard Brook Forest is a Cool Temperate forest, situated on the White Mountains in north-eastern United States. It has a short warm summer but long cold winter during which temperatures may go below freezing point. The dominant plant species are deciduous, the woody material of which comprises a much higher percentage of biomass than that of the garrigue. When we compare the two ecosystems, we can see that in a scrubland community such as the garrigue, a large percentage of the mineral ions is contained in the litter, from which they will be released for recycling as the litter decomposes. By contrast, in the forest ecosystem, the proportion of mineral ions in the biomass is very great. Only a small percentage is contained in the litter for recycling. These results show that the rate of processes in this scrubland is greater than in the deciduous forest of the Cool Temperate region.

c) Litter decomposition: succession of the mycoflora

Successional studies of the mycoflora during decomposition have been made on different parts of the living plants and on different kinds of litter. Again the most intensive studies have been made on angiosperms. Keener (1951), Smit and Wieringa (1955), Pugh and Buckley (1971b), Ruscoe

(1971) and Norse (1972a) have studied the fungal flora in buds and the living leaves. Studies have been made on leaf litter of Fagus crenata by Saito (1956), Quercus robur by Witkamp (1960), Quercus petraea, Betula verrucosa, Corylus avellana and Fraxinus excelsior by Hering (1965), Fagus sylvatica by Hogg and Hudson (1966), Eucalyptus regnans by Macauley and Thrower (1966), Acer saccharinum, Ulmus americana and Fraxinus pennsylvanica by Novak and Whittingham (1968), and Quercus sp., Coryleus avellana and Carpinus betulus by Remacle (1971). Hudson (1968) has given a brief review of studies since 1950, while Bell and Jensen (1974) have given an extensive review of fungi on herbaceous and tree litter.

Studies of succession have also been made on coniferous litter by Ward (1952), Kendrick (1957), Hayes (1965b) and Bransberg (1969). An extensive review has been given by Millar (1974).

The broad conclusion from these studies is that there is a successional change on the litter from a mycoflora of the phylloplane to a mycoflora of the soil. The primary colonizers are the common saprophytes which may be members of the phylloplane mycoflora or air-borne forms which become active at leaf senescence. These are able to decompose cellulose and to a certain extent, lignin. They are succeeded by secondary colonizers which are sugar fungi, predominantly the Mucorales. At the last

stage of decomposition, tertiary colonizers which are able to decompose the complex lignin compounds become predominant. The pattern of successional change is similar in herbaceous, deciduous and coniferous species, and many of the fungi found are common to all these substrates.

d) Litter decomposition: succession of the fauna

Studies on the fauna have also been made, but most of the work has been on the role, activity and population of the fauna (mainly the arthropods) while successional studies have rarely been made. The role of arthropods in litter decomposition has been studied by Crossley and Hoglund (1962), Edwards and Heath (1963), Witkamp and Crossley (1966), Edwards, Reichle and Crossley (1970), Heal and Chapman (1972), Asmus, Ferringini and McBrayer (1976b). The role of the fauna is that they fragment plant litter making available more surface area for micro-organism colonization; they leave faecal materials which become substrates for micro-organism growth. They may chemically decompose some of the organic compounds in litter and hence transform these into humic substances. Their movement through the litter and soil help to mix the organic and mineral components of the soil.

Recent studies on the arthropod population of the forest floor have been made by Dugdale (1974), McColl (1975) and Wiegert (1974). The most abundant arthropods are the Acari and Collembola. Among the Acari the

Cryptostigmatic mites are the most numerous. The ecology of micro-arthropods in litter and soil has been reviewed by Kühnelt (1961) and Wallwork (1970).

Successional studies have been made by Crossley and Hoglund (1962), Crossley and Witkamp (1964), who observed that the species diversity increased as litter became progressively decomposed, but Anderson (1975) reported that certain species became established early in the process and no new species colonized the litter at later stages. Moeller (1965) suggested that successional change was a result of seasonal factors.

Harding and Stuttard (1974) have reviewed the feeding habit, significance, and other aspects of microarthropods in litter decomposition. Edwards (1974) has given a review of the role and population of macroarthropods in decomposition. The assessment of the relative importance of macroarthropods in litter breakdown can only be approximate in view of the wide variation in the number, habit and type of food, and the lack of knowledge on their ecology and physiology. However, from available studies, it can be estimated that the group as a whole accounted for about one third of the consumption of total litter. They seem to play a more important part than the microarthropods. The role of nematodes and other aspects in decomposition has also been reviewed by Twinn (1974). Although nematodes may be subservient to the microflora in the decomposition

process, their high rate of intake but low assimilation may result in an increased amount of substrates for other organisms, and thus lead to a more rapid rate of transfer and recycling of nutrients.

2. The present investigation

a) Production and decomposition of litter, and the rate of release of cations

The annual litter production of 375.8 g m^{-1} at Site 1 was about 50.5% of the standing crop at that site. Therefore, the turn-over of the standing crop took about two years. The annual litter production of 351.7 g m^{-1} at Site 2 was about 37.4% of the standing crop at that site. The period of turn-over therefore was a little longer than that of Site 1, taking two years and eight months.

From the present study it was observed that the senescence and fall of leaves occurred throughout the year with peak fall at the beginning and end of the dry season, in October and March respectively. The rate of loss of dry weight and nutrient ions from the litter was very slow during the dry season, and the main loss began at the start of the wet season. Consequently, the loss of dry weight over a period of 12 months by leaves that fell at the beginning of the dry season was similar to the loss during 6 months from leaves that fell at the end of the dry season (= start of wet season). The percentage dry weight remaining for litter samples set

out in the dry and wet seasons was 61.98 and 62.24% respectively (Table 6.1).

The rate of loss of cations was much faster than the loss of dry weight (Table 6.1). Only 12.67% of the original sodium remained in the dry-season litter and 2% in the wet-season litter at the end of the experiment. The loss of potassium was also rapid, only 6.68% of the original content remaining in the dry-season litter and 9.15% in the wet-season litter. Thus nearly all of the sodium and potassium was lost by leaching during one rainy season. The effect of leaching was not so great in the case of magnesium: 74% was lost in a year with a dry and a wet season, and only 46% was lost in one wet season; so that the remaining magnesium amounted to 26% and 54% respectively. Calcium was released much more slowly: 63.72% of the initial content still remained after one year. Moreover, the addition during the rainy season made the situation more complicated. If the addition of calcium came from the rain and surface runnoff, the litter layer had the effect of retaining the calcium and retarding its rate of effective release.

The rate of loss of dry weight (decomposition) and the rate of release of the cations from Rhodomyrtus litter have been calculated for Site 2 and are summarized below.

I. Total standing crop of foliage of all species at Site 2 at harvest (23 March, 1978) = 9400 kg ha^{-1}

Standing crop of Rhodomyrtus foliage = 2780 kg ha^{-1}

Total *Rhodomyrtus* litter = 1040 kg $ha^{-1}yr^{-1}$

(assuming litter fall per species is proportional to standing crop of foliage).

II. Rate of decomposition of *Rhodomyrtus* litter in the dry season = 395 kg $ha^{-1}yr^{-1}$

III. Rate of release of cations

Cation content in kg ha^{-1}	Na	K	Mg	Ca
i) In standing crop of *Rhodomyrtus* at harvest	1.44	18.40	2.97	10.55
ii) In *Rhodomyrtus* leaf litter	0.59	8.30	1.21	3.56
iii) $\frac{\text{Ion in litter}}{\text{Ion in standing crop}} \times 100\%$	41.0	45.1	40.9	33.7
iv) Ion released from *Rhodomyrtus* litter per year	0.52	7.75	0.82	1.29
v) Percentage of ion in standing crop of foliage released per year	36.1	42.1	27.6	12.2

The results at (v) serves to emphasize the comparative immobility of calcium (and magnesium to a lesser extent) in the biotic part of the ecosystem. At Site 2, *Rhodomyrtus* contributes about 30% of the standing crop of foliage. It follows that in the scrubland as a whole the quantities of dry matter and cations being released might be about three times the amounts cited in the foregoing table.

When the cation content of *Rhodomyrtus tomentosa* in the present study is compared with that of *Quercus coccifera* in the garrigue, we can see that *Q. coccifera* has a higher content of cations. However, the percentages of cations

contained in the leaf litter of the two species are broadly comparable (30 - 50%), except that the litter of Q. coccifera contains a much higher percentage of calcium (79.7%) than does the litter of Rhodomyrtus. The greater amount of available calcium in Q. coccifera can be attributed to the fact that the soil on which the garrigue grows has developed from calcareous rock. Since both Rhodomyrtus tomentosa and Quercus coccifera are scrubland species, it might be expected that the rate of processes such as litter fall would be similar in the two communities. However, the hot and dry summer experienced by the garrigue would probably impede decomposition.

In comparing the Rhodomyrtus scrubland with the forest at Hubbard Brook a similar pattern of decomposition and release of cations can be discerned, even though the percentage of cations in the forest litter is appreciably less. The rate of loss of dry weight in Rhodomyrtus tomentosa (38% yr^{-1}) is similar to that of Acer saccharum (40% yr^{-1}) and Fagus grandifolia (32% yr^{-1}) in the Forest Ecosystem. Therefore, from the foregoing comparison, we may conclude that in general the rate of processes of decomposition in scrubland of the Sub-tropical region are faster than in Cool Temperate forests. The Cool Temperate forest is continuously accumulating mineral ions in the biomass with a small percentage loss from the litter.

b) The process of decomposition

When senescent leaves were placed on the ground, the process of decomposition began. During the dry season the leaves started to lose moisture to the atmosphere. Destruction of chlorophyll occurred, exposing the reddish color of the other pigments. The texture of the leaves changed, and they became progressively more brittle. If the leaves were placed on the ground in the dry season, there was a very slow rate of loss in dry weight and nutrient ions. However, if placed in the wet season, the rate of loss in dry weight was accelerated and the cations were subject to rapid leaching. Concurrently, the mycoflora of the freshly fallen leaves became active. Many leaf spots caused by fungal growth were observed. The leaf mycoflora was joined by new colonizers from the underlying litter. Eventually, fungi common in upper layers of soil replaced those originally present on the leaves. This sequence of change is similar to that observed by other workers on successional studies as mentioned in the literature review. While these processes were occurring, the litter was colonized by the micro- and meso-fauna which were mainly the micro- and macro-arthropods. However, the variety of species colonizing the litter in the early stages was not great, probably because the litter was relatively dry in the

dry season, or because it contained compounds unpalatable to the animals as suggested by many other workers. As the litter decayed more, the species diversity increased. An increase in species diversity has also been reported by Crossley and Hoglund (1962) and Crossley and Witkamp (1964). The increase in species diversity in the present study may be due to a greater variety of niches provided by more fungal growth, and to an increased degree of fragmentation and higher moisture content of the litter. Gasdorf and Goodnight(1963) also affirmed that litter is essential in providing habitats for the fauna. Litter offers food for the phytophagous species which are detritus-feeders, having chelicerae for grasping and complex mouthparts for chewing. Fungal growth on litter offers food for the saprophagous species such as nematodes and some species of mites. Litter also gives protection from predation (for example, insects from spiders). On the other hand, the body surface and faecal pellets left by the fauna themselves offer substrates for fungal growth (for example, Aspergillus sp. grew on the dorsal surface of weevils). Thus, litter with its associated mycoflora and fauna forms a self-sustained community. The species composition of the community is dynamic, and changes with inputs in the form of freshly fallen litter and with outputs due to release of organic compounds and nutrients to the underlying soil. The process of litter decomposition

is summarized in Figure 6.1, in which the percentages of dry weight and cations remaining in coarse and fine-mesh bags are averaged (for drawing the graphs), since the magnitude of loss was similar from bags of two different mesh size; these results are presented also in Table 6.1. The main points emerging are that rapid loss in dry weight and mineral ions is initiated at the beginning of the wet season. Therefore, the rate of decomposition in the wet season is much faster than in the dry season. As litter decays progressively, there is a successional change from a diverse mycoflora to a simpler one with few dominant species. By contrast, the change in the fauna is from few families of animals to a larger number of families.

From the present study on succession, the role of the mycoflora was envisaged as being to break down complex organic compounds. Destruction of the leaf skeleton, which was observed at the seventh collection in the dry-season litter, coincided with the peak abundance of Trichoderma spp. which has the ability to decompose cellulose. The appearance of Mucor spp., after Trichoderma spp., suggested that Mucor spp. may act as secondary colonizers which utilize the products of Trichoderma. The role of Mucorales as secondary colonizers on both broad-leafed and coniferous litter has been suggested by many other workers.

Although a number of functions of the fauna in litter break-down have been suggested, as discussed in the literature review, the role of the fauna in the present study was seen as bringing about the physical fragmentation of the litter. Evidence came from the observation that the rate of loss of dry weight and cations was more or less similar in both caorse- and fine-mesh bags, but the degree of fragmentation was very much greater in the coarse-mesh bags which allowed entry of larger animals such as some families of Coleoptera. Therefore, the degree of fragmentation has a close relation with the number and diversity of the animals. The greatest degree of fragmentation occurred in Collection No. 11 (the second last collection), with which is associated the greatest number of animals (Table 5.1), and the greatest loss in dry weight was also recorded in this collection because the highly fragmented material was lost through the holes of the mesh bags.

Thus, during litter decomposition the interaction is a very complex one. Both the mycoflora and the fauna fed on the litter. The mycoflora and the fauna interact among themselves. Growth of the mycoflora provided the fauna with food and micro-habitats. Physical fragmentation of litter and excretion of faecal pellets by the fauna provided

the mycoflora with additional substrates for growth. The biochemical activity of the mycoflora and the physical activity of the fauna together brought about the decomposition of litter, which was influenced to a great extent by environmental factors and particularly by moisture content. Water, either in the form of rainfall or as moisture in the tissue, accelerates the rate of loss of dry weight and the leaching of cations. Furthermore, it affects the occurrence and activity of many groups of animals.

Although research on litter has been very extensive, our understanding of the processes of litter production, decomposition, subsequent humification and the eventual recycling of its components is still far from complete. There is a need to synthesize and intergrate the vast amount of specific results obtained in order to construct a generalised pattern of the whole process; and this is particularly true of the tropics.

Figure 6.1 Integrated summary showing the loss of dry weight and cations, with the concomitant occurrence of the most abundant fungi and animals, and the march of rainfall and maximum / minimum temperature.

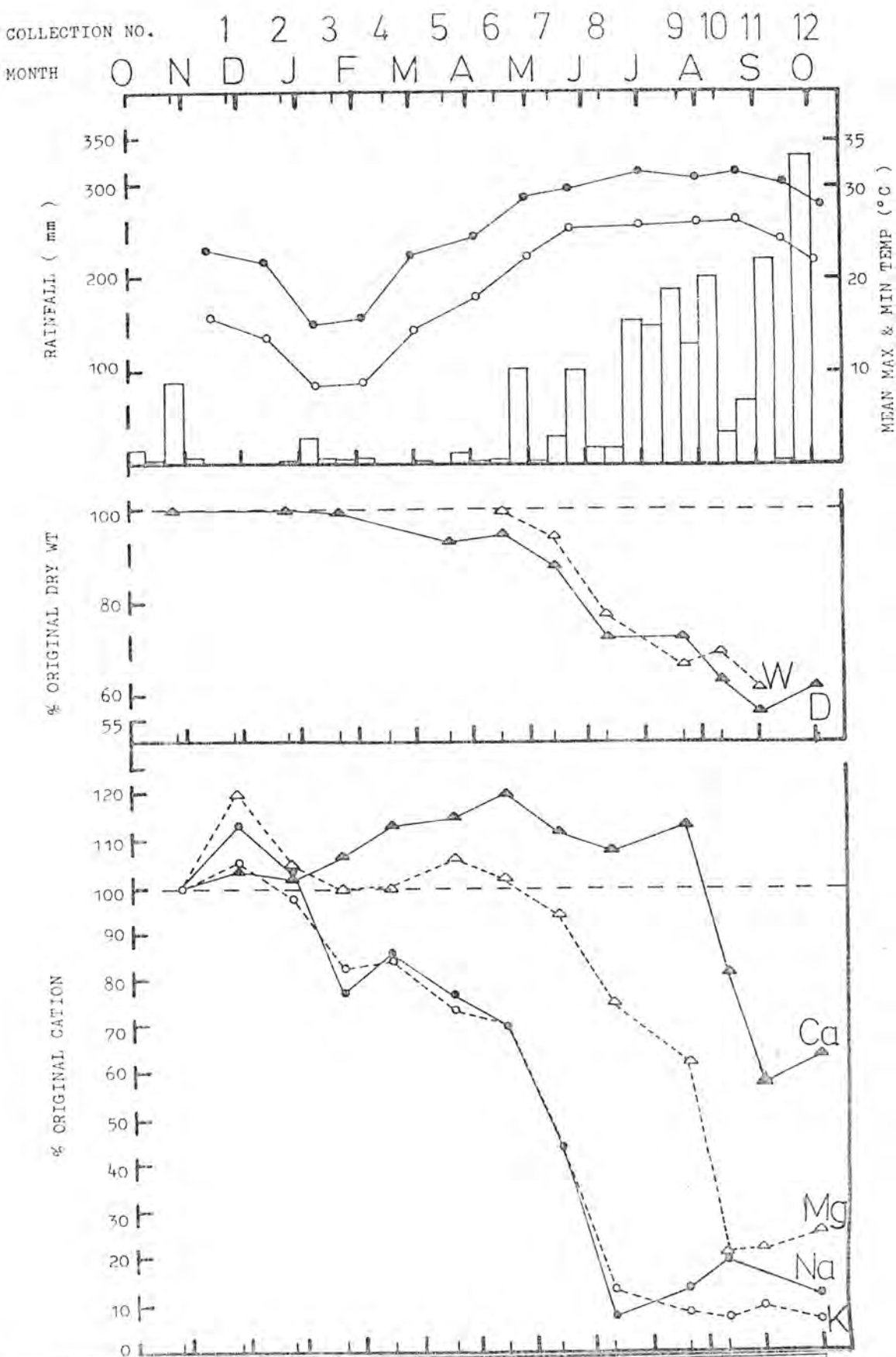
D : Litter samples set out at the start of the dry season.
W : Litter samples set out at the start of the wet season.

Abundance of fungi and animals :

——— <30% frequency of fungi or <20 individual animals

═══ 30-50% frequency of fungi or >20 individual animals

≡≡≡ >50% frequency of fungi.



A. Surface colonizers
1. Sterile sp. B
2. Pestalotia sp. A
3. Fusarium sp. A
4. Pencillium thomii
5. Phialophora fastigiata
6. Pencillium sp.
7. Trichoderma viride
8. Mucor hiemalis
9. Trichoderma glaucum
10. Trichoderma spp.
11. Mucor spp.
12. Trichoderma konigii
13. Mucor circinelloides

B. Internal colonizers
1. Colletotrichum sp. A
2. Sterile sp. D
3. Phomopsis sp. A
4. Phomopsis sp. B

A. Insecta
1. Blataria Blattidae
2. Diptera Mycetophilidae
3. Diptera Psychodidae
4. Diptera Chironomidae
5. Larval Lepidoptera
6. Larval Coleoptera
7. Collembola Entomobryidae
8. Larval Diptera
9. Collembola Sminthuridae
10. Hymenoptera Formicidae

D. Malacostraca
1. Isopoda Porcellionidae

E. Arachnida
1. Mesostigmata Phytoseiidae
Typhlodromus
2. Mesostigmata Ameroseiidae
Ameroseius
3. Astigmata Acaridae
Tyrophagus
4. Cryptostigmata Oribatulidae

Table 6.1 The mean percentage of dry weight and cations remaining.

Date of collection	Rainfall (mm) for previous 28 days	Dry wt.	Sodium	Potassium	Magnesium	Calcium
Dry Season						
1976. 26 Nov	30.7	-	113.29	105.22	119.99	103.94
23 Dec	0	99.79	104.16	98.00	105.79	102.46
1977. 20 Jan	28.0	99.20	77.49	82.51	100.94	107.52
15 Feb	5.9	-	85.93	84.55	101.43	113.72
17 Mar	2.9	93.45	77.11	73.79	106.90	115.78*
14 Apr	16.1	95.04	69.98	70.52	102.10	120.12
12 May	106.1	88.22	44.03	43.92	94.47	112.83
9 Jun	151.9	72.83	7.53*	13.30	75.52	108.75
19 Jul	348.4	73.02	13.54	8.48	62.14	114.37
10 Aug	464.8	63.59	20.13*	7.40	21.88*	82.66*
1 Sep	128.4	56.85*	65.26	10.02	21.97	58.39
30 Sep	487.3	61.98	12.67	6.68	26.12	63.72
Wet Season						
1977. 12 May	106.1	94.63	49.42	64.66	79.33	149.12
9 Jun	151.9	77.77	10.81	29.52	88.43	158.64
19 Jul	348.4	66.83	9.13	12.97	77.44	152.41*
10 Aug	464.8	69.90	2.61	9.87	48.53	147.13
1 Sep	128.4	62.24	2.71	9.15	54.22*	136.89

* The value in the coarse-mesh bags deviates much from that of the fine-mesh bags.

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APPENDICES

Appendix 4.1 The list and frequency of occurrence of fungi in fresh senescent leaves (control collections).

Month	25/10/76	26/11	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	Control	1	2	3	4	5	6	7	8	9	10	11	12
I. Phycomycetes													
Mucor hiemalis						4/25[a]; -							
II. Ascomycetes													
Glomerella cingulata	- ;1/30[b]												
Penicillium thomii	1/33; -			2/16; -	- ;2/13								
Trichosphaeria sp.													1/35; -
Unknown sp. A						- ;3/12							
III. Fungi Imperfecti													
Alternaria sp.	- ;3/30				2/19; -	3/25; -				2/22; -			
Aspergillus niger	- ;2/30	1/29; -		1/16;3/15			- ;1/9	1/17; -	3/25; -	5/22; -	3/20; -	3/20; -	3/35; -
Aspergillus sulpheus												1/20; -	
Aspergillus variecolor	- ;2/30												
Botryodiplodia theobromae									2/25; -				
Botryosphaeria ribis													1/35; -
Chlamydomyces sp.		1/29; -											
Cladosporium tenuissimum					- ;1/13								
Colletotrichum sp. A	1/33;14/30			- ;5/15	1/19;5/13	- ;4/12	- ;4/9		- ;2/7	- ;3/6	- ;2/8		1/35; -
Colletotrichum sp. B										- ;1/6	- ;4/8	- ;6/9	- ;10/11
Curvularia eragrostidis	1/33; -				3/19; -			1/17; -					

Appendix 4.1 (continued)

Month	25/10/76	26/11	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	Control	1	2	3	4	5	6	7	8	9	10	11	12
Curvularia geniculata												1/20; -	2/35; -
Curvularia sp.	1/33; -						1/18; -				1/20; -		1/35; -
Cytospora sp.*				1/16; -									
Drechslera turcica		1/29; -										1/20; -	
Fusarium oxysporum	3/33; -	2/29; -				1/25; -					1/20; -		3/35; -
Fusarium solani		1/29; -				2/25; -							
Fusarium sp. A	4/33; -				2/19;2/13	2/25;1/12		4/17; -			/20; -		2/35; -
Fusarium sp. B						1/25; -							
Gliocladium roseum						2/25; -							
Libertella sp.	- ;2/30												
Macrophoza sp.								1/17; -				2/20; -	
Neurospora crassa				1/16; -	1/19; -	- ;1/12							
Nigrospora sp.	1/33; -			2/16; -	1/19; -	2/25; -					1/20; -		
Penicillium frequentans													1/35; -
Penicillium sacculum												1/20; -	1/35; -
Penicillium sp.	2/33;3/30	1/29; -		1/16; -		- ;2/12		1/17; -			1/20; -	1/20; -	
Pestalotia spp.	6/33; -	10/29; -		5/16; -		3/25; -	5/18; -	4/17; -	4/25; -	4/22;1/6	2/20; -	4/20; -	6/35; -
Phialophora fastigiata	1/33; -			1/16; -	1/19; -	3/25; -	2/18; -	2/17; -	3/25; -	1/22; -	2/20; -	1/20; -	2/35; -
Phomopsis psidii								2/17; -			- ;1/8		
Phomopsis sp. A				- ;2/15								- ;1/9	

Appendix 4.1 (continued)

Month / Coll. No.	25/10/76 Control	26/11 1	23/12 2	20/01/77 3	15/02 4	17/03 5	14/04 6	12/05 7	09/06 8	19/07 9	10/08 10	01/09 11	30/09 12
Trichoderma hamatum										3/22; -	2/20; -		1/35; -
Trichoderma harzianum											1/20; -		
Trichoderma konigii					- ;1/13		3/18; -				1/20; -		2/35; -
Trichoderma viride	1/33; -				3/19; -				7/25; -	1/22; -			2/35; -
Trichoderma spp.	1/33; -	4/29; -		- ;2/15	1/19; -		1/18; -		5/25; -	2/22; -	2/20; -	1/20; -	2/35; -
Unknown sp. B					- ;1/13								
IV. Sterilia Mycelia													
Species A				- ;1/15					- ;2/7				
Species B	9/33; -	2/29; -		2/16; -			1/18; -		2/25; -	1/22; -	1/20; -	3/20; -	1/35; -
Species C	- ;2/30												
Species D	- ;1/30			- ;1/15			1/18;1/9		- ;2/7				
Other sterile spp.	1/30;2/30	6/29; -		- ;1/15	2/19;1/13	2/25;1/12	4/18;3/9	1/17; -	4/25;1/7	3/22;1/6	1/20;1/8	1/20;2/9	2/35;1/11

a first fraction: surface colonizers

b second fraction: internal colonizers

* has not been reported on Rhodomyrtus previously.

Appendix 4.2 The list and frequency of occurrence of fungi in litter samples set out in the dry and wet seasons.

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7	8	9	10	11	12
							1w	2w	3w	4w	5w	6w
I. Phycomycetes												
Backusella circina											5/26[a]; -	
									3/18; -		1/21; -	
Mucor circinelloides												9/35; -
Mucor genevensis												1/35; -
Mucor hiemalis				6/22; -	14/31; -					5/22; -	2/26; -	3/35; -
									2/18; -			
Mucor saturninus			2/22; -									
Mucor spp.						1/17; -		4/27; -	2/13; -	6/22; -		9/35; -
									1/18; -			
Rhizopus sp.			2/19; -									
II. Ascomycetes												
Penicillium thomii		6/25; -	2/19; -	2/22; -		1/17;2/13[b]						
Penicillium wortmanii											3/21;3/27	
Species forming ascogenous coils only											- ; 2/27	
Unknown sp. A						1/17; -						
III. Fungi Imperfecti												
Acremonium sp.									- ;4/23	1/22; -		

Appendix 4.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7 1w	8 2w	9 3w	10 4w	11 5w	12 6w
Alternaria sp.		- ;1/16										
Aspergillus niger									1/13; -	2/22; -		
Aspergillus sulpheus								1/27; -				
							1/24; -					
Beltraniella nilgirica										- ;1/6		
										- ;10/22		
Botrydiplodia theobromae									2/18; -			
Botryosphaeria ribis		1/25; -			- ;1/21							
Colletotrichum sp. A	- ;8/24	- ;3/16	- ;4/14	- ;4/17	- ;3/21	- ;3/13	- ;4/35					
							- ;4/29	- ;1/7	- ;3/8			
Colletotrichum sp. B		- ;1/16					- ;1/35					
Curvularia eragrostidis							1/24; -					
Cytospora sp.*			- ;1/14									
Dendrodochium sp.									- ;3/23	- ;1/6		
Epicoccum purpurascens					1/31; -							
Fusarium oxysporum				2/22;3/17	- ;2/21							
							5/24; -		1/18; -	2/12; -		
Fusarium solani	2/30; -			2/22; -								
									1/18; -	- ;2/22		

Appendix 4.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7	8	9	10	11	12
							1w	2w	3w	4w	5w	6w
Fusarium sporochioides									1/18; -			
Fusarium sp. A	3/30; -			3/22; -	- ;1/21	1/17; -		2/27; -				1/35; -
							3/24; -		2/18; -	5/12; -		
Fusarium sp. B							2/24;2/29					
Gliocladium roseum										1/22; -		
Macrophoma sp.							- ;2/29					
Neurospora crassa					1/31; -							
Nigrospora sp.		1/25; -	2/19; -									
Parasympodiella laxa											- ;14/27	
Penicillium citrinum							1/20;					
Penicillium expansum			- ;2/14									
Penicillium sp.	3/30; -	1/25;1/16			- ;3/21	2/17; -		1/27; -			3/26; -	
Pestalotia spp.	10/30; -	6/25;3/16	4/19;2/14	- ;1/17	- ;1/21	3/17; -		3/27; -				
							2/24; -					
Phialophora fastigiata	4/30; -	4/25;1/16	1/19; -		12/31;4/21	1/17; -		5/27; -				
							7/24;6/29	- ;2/7				
Phomopsis psidii			- ;2/14		- ;1/21		- ;5/25		- ;4/23	- ;2/6		
							2/24;1/29					
Phomopsis sp. A	- ;2/24	- ;1/16		- ;2/17	- ;1/21	- ;1/13	- ;6/35	- ;8/17	- ;3/23	- ;1/6		
							- ;4/29	- ;3/7	- ;3/8			

Appendix 4.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7	8	9	10	11	12
							1w	2w	3w	4w	5w	6w
Phomopsis sp.B							- ;2/35		- ;1/23			
									- ;2/8			
Scolecobasidium humicola											- ;7/5	
										- ;6/22	- ;3/27	
Trichoderma album								3/27; -				
Trichoderma glaucum							9/20; -					
Trichoderma hamatum											2/21; -	
Trichoderma harzianum			2/19; -									
Trichoderma konigii											5/26; -	4/35; -
							1/24; -				3/21; -	
Trichoderma viride			3/19; -	3/22; -		- ;3/13	6/20; -	1/27; -				
									4/18; -		1/21; -	
Trichoderma spp.					1/31; -	3/17; -		3/27; -	4/13; -	3/22; -	6/26; -	2/35; -
										5/12; -	8/21; -	
Verticillium sp.		- ;1/36										1/35; -
IV. Sterilia Mycelia												
Species A			- ;1/14					- ;2/17				
							- ;2/29					
Species B	3/30; -	4/25;1/16										
Species C		- ;1/16	- ;1/14				- ;2/35					
Species D	- ;11/24	- ;2/16		- ;2/17	1/31;2/21	- ;1/13			- ;2/23			
							- ;1/29					
Species E					1/31; -				3/13; -			
Other sterile spp.	5/30;3/24	2/25; -	3/19;1/14	4/22;5/17	2/21; -	4/17;3/13	4/20;6/35	4/27;7/17	3/13;6/23	4/22;1/1	5/26;2/5	5/35; -
							- ;6/29	- ;1/7	1/18; -	- ;4/22	3/21;5/27	

a first fraction: surface colonizers

b second fraction: internal colonizers

_ fungi on litter put out in the wet season

* has not been reported from Rhodomyrtus previously.

Appendix 4.3 The list of fungi from surface soil under litter samples in the dry and wet seasons.

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7 1w	8 2w	9 3w	10 4w	11 5w	12 6w
I. Phycomycetes												
Mucor sp.	1/20[a]											
Rhizopus sp.								1/12[b]				
II. Ascomycetes												
Penicillium brefeldianum										1/15		
Penicillium thomii		2/13	4/18					1/13		2/15		
Penicillium wortmanii		1/13	1/18	1/11	3/7		2/12 3/17	1/13 2/12		1/15	4/12 5/15	
III. Fungi Imperfecti												
Dreschslera turcica	1/20											
Fusarium oxysporum								2/12				
Neurospora crassa							2/12			1/15		
Penicillium expansum							1/12					
Penicillium sp.	1/20		4/18							1/15	2/12	
Phialomyces macrosporus			1/18							2/15	2/15	
Trichoderma hamatum							6/12					
Trichoderma konigii			3/18		2/7		2/17			2/15	1/15 3/12	
Trichoderma viride	16/20	8/13	1/18				1/17 1/12	1/12 7/13			2/15	
Trichoderma spp.			1/18				7/17 2/12					
Unknown sp. A			1/18					3/12			3/15	

a under litter samples in dry season

b under litter samples in wet season

Appendix 5.1 The list of animals captured in the field .
(Classification of the Class Arachnida follows Evans, Sheals and Macfarlane, 1961)

Year	76	77													78		
Month	12	02	03	04	05		06	07	08	09		09	11	11	01	03	
Day	23	15	17	14	12		09	19	10	01		30	03	28	26	23	
Coll. No.	2	4	5	6	7		8	9	10	11		12	13	14	16	18	Total no. of
Site	D	D	D	D	D	S1	D S1	D	S1	D	S1	D S1	S1	S2	S1	D	animals
A. Class Insecta																	
I. Immature Insects																	
Order Collembola																	
Entomobryidae										4							4
Sminthuridae										1							1
Order Coleoptera (larvae)										14			1		1		16
Order Diptera (larvae)																	
Chironomidae										1							1
Ceratopogonidae										2							2
Order Lepidoptera (caterpillar)							1										1
I. Adult Insects																	
Order Blataria																	
Blattidae			1				1		2								4
Order Coleoptera																	
Chrysomelidae			1		1												2
Curculionidae								1									1
Order Dermaptera							1										1
Order Diptera																	
Calliphoridae	1																1
Mycetophilidae														1			1
Order Hemiptera																	
Reduviidae		1										1					2
Order Hymenoptera																	
Formicidae			1(5)	1	1					5							13
Order Orthoptera																	
Phasmidae									1								1
B. Class Chilopoda										1							1
C. Class Malacostraca																	
Order Isopoda																	
Porcellionidae								1	3	1	3	2					10
D. Class Arachnida																	
Subclass Acari																	
Order Astigmata																	
Acaridae (Tyrophagus)								13									14
Order Prostigmata																	
Chelytidae								1									1
Order Cryptostigmata																	
Belbidae (Belba)										1							1
Oribatulidae										2							2
Subclass Pseudoscorpionidae																	
Neobisiidae (Microcreagris)										1							1
Subclass Araneae			(5)		3		(1)	1	1	1		1 1			1	1	16

key : D=site for decomposition studies . S2=site2for litter production
S1=site 1 for litter production ( )=immature forms

Appendix 5.2 The list of animals from the extraction of litter samples in the dry and wet seasons.
(Classification of the Class Arachnida follows Evans, Sheals and Macfarlane, 1961)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.[1]	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
A. Insecta												
I. Immature Insects												
Collembola												
Entomobryidae							1/	1/5	4/3		5/1	
Sminthuridae								21/	/1	2/	1/8	11/
Neanuridae								1/				
Poduridae						1/					1/1	
Coleoptera (larvae)						2/		/1			6/1	2/
Diptera (larvae)												
Chironomidae								3/5		3/	/1	
Other families											14/	
Hymenoptera (larvae)												
Formicidae											6/	
Lepidoptera (larvae)							1/	2/	1/	1/1	1/	1/
Indeterminate												
larvae (L1)										2/		1/
eggs								1/	3/			

Appendix 5.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
II. Adult Insects												
Coleoptera												
Curculionidae								/1			1/1	
Mycetophagidae											1/	
Scarabaeidae						1/						
Scolytidae							1/					
Silvanidae											1/	
Staphylinidae					1/						1/1	1/
Dermaptera								1/				
Diptera												
Calliphoridae						1/						
Cecidomyidae					1/	1/	2/				/1	1/
Ceratopogonidae					1/		3/1	/6			2/	
Chironomidae			1/		3/	1/		/1	/7	8/1	12/2	
Chloropidae					2/	1/	1/2	/2			1/	
Mycetophilidae			1/	1/	2/	1/					3/1	2/
Psychodidae				1/	1/		2/1	1/1			1/	4/
Tethinidae							2/					

Appendix 5.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Hemiptera												
Delphacidae							1/1	1/				3/
Dipsocoridae							/1					
Jassidae			2/					2/1			/1	1/
Lygaeidae						1/						
Miridae							1/					
Reduviidae					1/							
Hymenoptera												
Braconidae					1/	1/					/1	
Formicidae 1								/2			25/2	
Formicidae 2								/1			1/	
Mymaridae 1					1/		/1				1/	
Mymaridae 2						1/	3/		/1			
Vespoidae											2/	
Blataria												
Blattidae 1					3/							1/
Blattidae 2			2/	1/	1/	3/	/2			3/		
Pscoptera												
Peripsocidae							/3					

Appendix 5.2 (continued)

	Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
	Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
	Thysanoptera												
	Thripidae & Phloeothripidae				1/	1/	2/	/4					
B.	Diplura												
	Campodeidae						2/	1/2	3/				
C.	Malacostraca												
	Isopoda												
	Porcellionidae								11/1	4/	1/	4/2	5/
D.	Arachnida												
	I. Acari												
	Astigmata												
	Acaridae												
	Tyrophagus sp.							1/	/9	3/14	5/4	3/4	
	Prostigmata												
	Cunaxidae												
	Neocunaxoides sp.									/1			

Appendix 5.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Trombidiidae												
Allothrombium sp.										1/		
Trombidiformes												
Rhagidia sp.											3/	
Erythraeidae												
Leptus sp.					1/							
Mesostigmata												
Ameroseiidae												
Ameroseius sp.						2/		6/	11/1	10/		1/
Ascaidae												
Asca aphidioides								1/19	2/	/1	1/8	
Eutrachytidae												
Eutrachytes sp.										/4	/3(1)[2]	3(1)/
Parasitidae & Veigaiidae												
Pa 1 & Veigaia sp.										4/	7/	
Phytoseiidae												
Typhlodromus 1 sp.	2/		1/			2/			/2			2/
Typhlodromus 2 sp.								/1	1/1	13/	/2	4(2)/
Phy 1												1/
Phy 2												1/

Appendix 5.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Podocinidae												
Podocinum sp.										1/	1/	
Gamasiphis sp.										2/		
Rh 1												1/
Cryptostigmata												
Belbidae												
Belba sp.											2/	1/
Be 1	1/										1/4	
Be 2									/1			
Plesiodameus sp.						1/		1/			1/	
Be 3												1/
Eremaeidae												
Er 1											1/	
Oribatulidae												
Or 1								28/6	7/5	31/4	1/8	10/
Pht 1								1/		/1	/3	
Immature Cryptostigmata								1/1	/1	7/	/6	3/

Appendix 5.2 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
II. Pseudoscorpionidae												
Chthoniidea												
Tyrannochthonuis sp.					1/	1/		1/	1/	/3		
III. Araneae												
Clubionidae											1/	
Linyphiidae											1/	
Ogelenidae												
Wadotes sp.											1/	
Scytodidae												1/
Indeterminate											/1	

1. Coll. Nos. 1-12 : Litter samples set out in the dry season.
   Coll. Nos. 1w-5w : Litter samples set out in the wet season.
2. ( ) : Immature forms.

Appendix 5.3 The list of animals from extraction of surface soil under litter samples.
(Classification of the Class Arachnida follows Evans, Sheals and Macfarlane, 1961)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.[1]	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
A. Insecta												
I. Immature Insects												
Collembola												
Entomobryidae	2	8	3		2		/1	/12	4/3	1/7	14/24	2
Sminthuridae								/2	1/1	/6	/8	1
Neanuridae									/2	1/1	2/1	
Poduridae	1	4	8						/1		1/	
Isotomidae	13											
Coleoptera (larvae)					3					/1	1/	2
Diptera (larvae)												
Chironomidae		1	1							/1		
Mycetophilidae			1			1					/1	
Other families		1								/1		
Hemiptera (nymph)												1
Homoptera												
Nephotettix	2											
Hymenoptera (larvae)												
Other families			1									

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Lepidoptera (larvae)									2/		/1	
Indeterminate												
Larvae (L1)											4/	
Larvae (L2)			8		3				1/			
II. Adult Insects												
Coleoptera												
Curculionidae								1/1				
Mycetophagidae											/1	
Pselaphidae											1/	
Scolytidae					1							
Staphylinidae							2/1					1/
Diptera												
Cecidomyidae				1			/1	/1			/1	
Ceratopogonidae						1/	2/2	/1			/4	
Chironomidae		1		1			1/		/1	/2	/3	
Chloropidae											/1	
Drosophilidae											/1	

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Ephydridae											/1	
Muscidae							1/					
Mycetophilidae			1			1					/1	
Phoridae				1								
Psychodidae					2		1/3				/1	1
Tethinidae				1								
Hemiptera												
Aphididae				1								
Delphacidae						1		1/1				
Jassidae							/1	/2				1
Miridae						1						
Coccoidea		1										
Hymenoptera												
Braconidae					1							
Cynipoidea												1
Formicidae 1					2	(9)[2]		1/4	6/	22/9	2/	
Formicidae 2							1/		/3		/8	

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Mymaridae 1						1			/1			
Mymaridae 2		1	1				2/4	/1			/2	
Platygasteridae									/1			
Blataria												
Blattidae 1				1			/1					
Blattidae 2							1/					
Thysanoptera												
Thripidae & Phloeothripidae	1					1	/2					
Isoptera												
Rhinotermiditae (Reticulitermes fukienensis)										3/		
B. Chilopoda	2								1/			
C. Diplura												
Campodeidae						7	/2		1/			2

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
D. Malacostraca												
Isopoda												
Porcellionidae											/(2)	
Oniscidae	1											
E. Symphyla								/1		/1		
F. Arachnida												
I. Acari												
Astigmata												
Acaridae												
Tyrophagus sp.							/1	/5	22/24	/1	1/2	1
Prostigmata												
Bdellidae												
B 1 (snout mite)							1/2		/1	/1		2
Cheyletidae												
Che 1	1											

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Cunaxidae												
Neocunaxoides sp.		1							1/		1/3	3
Cunaxa sp.									/1			
Cu 1									/2			
Nothroidea												
No 1		1	2					/1				9
Penthplodidae												
Pen 1	1											
Trombidiidae												
Allothrombium sp.						1		/1	1/1	/1	1/	
Pachygnathidae												
Pac 1	4											
Mesostigmata												
Ameroseiidae												
Ameroseius sp.									/1			1
Ascaidae												
Asca aphidioides	1		2						/1	/5	/2	
Asca sp.			1								1/	

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Eutrachytidae												
Eutrachytes sp.											/1(1)	1
Macrocheylidae												
Ma 1	4							/1	/2	/2		
Parasitidae & Veigaiidae												
Pa 1 & *Veigaia* sp.		4	1					/5			1/	1
Phytoseiidae												
Typhlodromus 1	1								4/3	/1	1/	2
Typhlodromus 2			1				/1					
Podocinidae												
Podocinum sp.									/1		/3	
Rhodacaridae												
Acugamassus sp.	17	8	12		3	1				/1	1/11	
Gamasiphis sp.												1
Uropadellidae												
Ur 1									/1			
M 1			1			1		/4		/4	1/2	
M 2								/2				

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
Cryptostigmata												
Galumnidae												
Allogalumna sp.		1	1		1	2		/1	/4	/6		1
Galumna sp.					1			/1	/2			
Belbidae												
Belba sp.												1
Be 1					2			/6	/1	/1	/10	22
Be 2					1	3		/3		/6		
Plesiodameus sp.	2	1	1						/3	/10	/2	11
Be 3							/1	/2				
Eremaeidae								/1		/1		1
Oribatulidae												
Or 1	4	2	13		2			/6	8/3	/23	1/4	2
Or 2			1					/4				
Phthiracaridae												
Paratritia sp.								/13	1/1	/3		5
Immature Cryptostigmata												
C 1								/1	/1	/3	/2	8
C 2										/3		4(15)
C 3								/2			/5	

Appendix 5.3 (continued)

Month	26/11/76	23/12	20/01/77	15/02	17/03	14/04	12/05	09/06	19/07	10/08	01/09	30/09
Coll. No.	1	2	3	4	5	6	7/1w	8/2w	9/3w	10/4w	11/5w	12
II Pseudoscorpionidae												
Chthoniidae												
Tyrannochthonius sp.			2						/1	/4	/1	1
III Araneae												
Ctenizidae												
Acattyma sp.											1/	
Linyphiidae												1
Oonopidae											1/	
Salticidae									1/			
Thomisidae										/1		
Indeterminate							/1	/1		/1	2/1	1

1. Coll. Nos. 1-12 : Litter samples set out in the dry season.
   Coll. Nos. 1w-5w : Litter samples set out in the wet season.
2. ( ) : Immature forms.